ENVIRONMENT AND PLANT DEVELOPMENT

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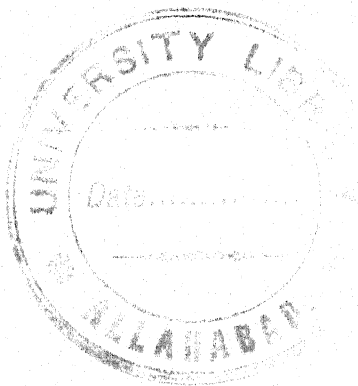
BY

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TRANSLATED AND EDITED
FROM THE SECOND GERMAN EDITION

BY

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LONDON
EDWARD ARNOLD & CO.
1931

TRANSLATOR'S PREFACE

PROFESSOR LUNDEGÅRDH needs no introduction to the present generation of botanists in England and America. He has been the pioneer, and he is the leader in a realm of research which may dominate the botany of to-morrow. It is to the coming generation of botanists, who may not be sufficiently familiar with German, that this translation is dedicated in the hope that it will stimulate interest in experimental ecology among English and American students.

In his letters to me, and in the introduction to the second edition, Professor Lundegårdh insisted that his book is not intended as a handbook, but as an outline of a new mode of research. To reproduce this spirit in the English translation it has been necessary to modify somewhat the arrangement of the German edition. I have eschewed voluminous foot-notes: the references have been assembled at the end of the book, and the relevant footnotes incorporated in the text. A few references, which can be found in other summaries mentioned in the text, have been omitted. Certain parts of the book, especially the more philosophical discussions in Chapters I and X, have been slightly condensed, and the numerous sub-titles, which are inappropriate in English, have not been included. In a few instances I have replaced examples from Scandinavian botany by examples more familiar to English readers.

In editing the book I have naturally made no attempt to comment on Professor Lundegårdh's statements, or to refer to certain fields of research he has omitted. Much of the discussion on nitrogen metabolism, for instance, assumes a different aspect in the light of recent work on the carbo-hydrate : nitrogen balance in plants; and recent work of the Californian school throws fresh light upon the relation of soil moisture to vegetation.

All the line drawings in the original are reproduced in the translation, and many of the photographs. The expense

of including the two maps is not justified in the English edition, since reference can always be made to Bartholomew's excellent meteorological atlas. Sundry minor errors in the German text and in the references have been corrected. Despite the omissions and changes, I hope to have preserved some of the stimulating spirit and clear vision of the original, —enough to induce younger botanists to read Lundegårdh's own work and to continue the research he has begun.

In conclusion I wish to record my thanks to the Botany department of the University of Chicago for its unfailing courtesy, and to Professor V. H. Blackman for his help in the earlier stages of the work. I am much indebted to Dr. E. H. M. Farries, who did some of the "spade work" of the translation, and to the publishers for their help and advice.

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PREFACE TO THE FIRST GERMAN EDITION

THE present book is the outcome of a series of lectures, which I delivered in the winter of 1923–4 in Brünn, at the invitation of the Minister of Education of Czecho-Slovakia and the Masaryk University. Many years ago, when I began to hold classes in practical physiological ecology at the ecological station at Hallands-Väderö, which I had founded, I took the point of view that the problems of Ecology and causal plant Geography can only be solved by experimental methods. This concept has been developed in a number of papers which my associates, my students, and myself, have published; and the exposition in the following pages is a development from this experimental work.

Though the realm of experimental ecology is still relatively undeveloped, it is being opened up so rapidly, and it has received so much study, that it cannot be confined to the limits of a small book. Only the salient features can be described. I have tried to deal especially with the most recent literature, and have not hesitated to treat in most detail those problems upon which I myself have experimental data. I hope by such presentation more clearly to focus the details without any loss of general perspective. I am of the opinion that ecological factors cannot be properly valued and measured without a knowledge of their physiological action. Every problem, therefore, has been treated from a physiological standpoint, and I have tried especially to bring into use certain general physiological laws, such as the law of the relative effects of factors.

It was in response to repeated requests of my audience that I undertook to publish this work. In that audience were many agriculturists and practical men. For this reason I have often referred to investigations in agriculture and forestry, from which many contributions to Ecology have come.

Almost all of the photographs have been taken at Hallands-

Väderö, and are intended to portray a number of northern plant societies. . . .

I wish to convey my most sincere thanks to the Minister of Education of Czecho-Slovakia, and the members of the faculty of Natural Science in Brünn, for their cordiality to me during my stay in the Republic. I wish also to thank the publisher, who so readily carried out my wishes as to the arrangement of the book.

<div align="right">H. LUNDEGÅRDH</div>

ECOLOGICAL STATION AT HALLANDS-VÄDERÖ,
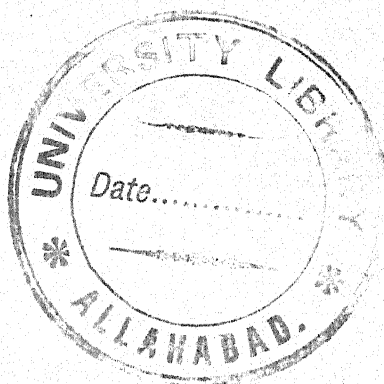   *June* 23, 1925.

PREFACE TO THE SECOND GERMAN EDITION

IN the four or five years which have elapsed since the first
edition appeared, the realm of experimental ecology has been
most intensively explored.   Especially in soil science, micro-
biology, and the study of the sociology of plants, the output
of literature has been immense.   No more attempt has been
made here than was made in the first edition to give an
exhaustive review of the literature.   The book is not intended
as a handbook, but is rather to give the principles of a certain
type of research.

Despite numerous additions to the literature, and a
thorough revision of the text, the general structure of the
book has been retained.   Those aspects of the subject in
which I have been particularly interested have been somewhat
extended.   By constant reference to the summaries of other
authors, I hope to have attained some equality of treatment
of the different fields.   Restrictions of space have precluded
a fuller treatment of the wide literature which deals with the
practical applications of the subject in forestry and in agri-
culture.

New text figures have been added, and two have been
redrawn.   Since the two maps [omitted from the English
Edition] are intended to give only a rough schematic outline,
it has not been considered necessary to improve them.

STOCKHOLM-EXPERIMENTALFÄLTET,
January, 1930.

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CHAPTER I

INTRODUCTION

IT is the aim of plant geography to describe and to map plant life over the earth. In every science, be it apparently purely descriptive, there arises the need for a causal understanding of the observed facts. It is not surprising to find, therefore, at the very outset of plant geography, the endeavour to establish a causal relationship between plant distribution and external conditions.

A. v. Humboldt, the founder of research in plant geography, was not content to enunciate the principles of classification of plant communities, but ventured to divide the earth into zones and regions, which should show a parallelism between climate and plant distribution. Griesebach (1872) had in mind the same aim in clearer form, when he took up the long unnoticed work of Humboldt. Griesebach tried to establish the boundaries of plant formations, and to discover whether there was any correlation between these boundaries and those of climate, such as isotherms. But the meteorological and physiological knowledge of that time was inadequate, and his efforts met with little success. Although much of the writing on plant geography published at that time (Schleiden, 1848; Kabsch, 1865) was nothing more than the results of indiscriminate plant collecting, the work of Humboldt was a really serious attempt to impose some system on the enormous variety of the earth's vegetation, and in doing so he distinguished definite external physiognomic characters in that vegetation. A number of distinguished investigators, Wahlenberg (1813, 1819), A. de Candolle (1855), Griesebach (1872), Engler (1879) and Drude (1890, 1913), have

thoroughly developed this floristic or physiognomic plant geography, and through their indefatigable labour we are acquainted to-day with the earth's vegetation as a whole.

In the course of its development the study of floristics has become more and more admixed with biological and ecological ideas. A mere systematics of forms, without any reference to plant habit, would be nothing but a dull catalogue. Griesebach's attempt, for instance, to use leaf form as a basis of classification, is quite useless. Only a concept of the form and anatomy of plants as an adaptation to life under definite external conditions will lead to a classification which groups under the same head plants which really live together.

The main ideas of ecological plant geography, while they are not concerned with the question of the origin of species, are bound up with the laws of the mutual antagonism of all living things. In the continuous fight against their neighbours and the outside environment, those forms succeed which are best "adapted" to the conditions of the habitat. The word "adaptation," used in this sense, is really descriptive. It might be illustrated by saying that one form is better adapted than another when it uses the energy at its disposal with more economy, and is better protected against unfavourable conditions.

The reason why the plant physiologist hesitated so long before attacking ecological problems is quite clear. The living organism displays so many simultaneous processes that it is impossible to follow them all at once. Accordingly there is in plant physiology a standard rule for experimental work which must be followed. The organism must be brought under constant conditions, and that factor alone varied whose influence is to be studied.

This exact physiology, which was developed by some of the best-known German workers, is the firm ground upon which all causal knowledge of plant life must stand. But this does not represent the ultimate goal of research. When a plant is brought into the laboratory for experiment it is removed from its natural environment, into a simplified environment, and perhaps upset altogether; and in the end nothing may be known of the part played in the natural life of the plant by the phenomena measured in the laboratory.

In the last decade, however, there has been an unmistakable movement on the part of physiologists toward ecology (Fitting, 1922). New methods, unknown in plant physi-

ology, have been developed, and the science has received the appropriate name of experimental ecology.

The aim of experimental ecology is the investigation of the plant's reaction to a given "constellation" of ecological factors, with a view to discovering how the plant behaves in its natural habitat. There exists no sharp distinction between this study and synecology, which investigates plant societies in the same way.

The final goal of every science is the causal explanation of observed natural phenomena. On this ground alone it would be impossible to stop at the mere floristic analysis of vegetation. The fact that we still know relatively little about the causal relationship between environment and vegetation is scant reason to deny the existence of such a relationship. On the other hand, it would be wrong to assume that the distribution of vegetation depends solely upon the present physical and chemical environmental conditions. The composition of a plant community is the product of an historical development, of an immigration (Clements, 1905) and of a struggle for existence among the colonists. Obviously in this process all circumstances which influence seed dispersal, etc., are of importance, and the investigator must take into account the influence of the plants upon one another, and upon the soil in which they are growing.

Now in a purely physiological investigation the worker endeavours to simplify his inquiry as much as possible, and to reduce his experiment to the minimum number of variables; but in experimental ecology he must reckon from the beginning with a great number of parallel processes. The phenomena one observes in Nature are always the resultant of the interaction of a number of more or less independent factors, and the investigator must consider these all together. The methods peculiar to experimental ecology may best be illustrated by a number of examples.

The environment of the plant can be broken up into a mass of ecological factors: the atmospheric factors—light, temperature, humidity, rainfall, and carbon dioxide, and the edaphic factors—the physical and chemical nature of the soil, its water content, salt content, hydrogen ion concentration, micro-flora, and so on.

In the investigations of photosynthesis, for instance, the plant physiologist concentrates upon the mechanism of decomposition of carbon dioxide, while the influence of light

intensity, chlorophyll content, carbon dioxide concentration, etc., are only studied in so far as is necessary for the elucidation of the inner mechanism. But these external factors and their influence are the main interest in ecology. The amount of carbohydrate formed by a plant at a given time depends upon a whole plexus of factors. For example, the resultant effect of any specific change in light intensity varies with the amount of carbon dioxide present, or with the amount of chlorophyll in the plant. Furthermore, one would imagine that the formation of carbohydrate would reach its optimum in the full light and high temperature of midday, but this is often not the case. For the increased transpiration often initiates a temporary closing of the stomata, and a consequent drop in carbon assimilation. While laboratory experiments, then, lead one to expect a maximum at midday in the assimilation curve, there is, under natural conditions, more often a depression at this time. Similarly, it is often forgotten in laboratory experiments on assimilation, that under natural conditions, a plant respires during the night a considerable part of the assimilate built up in the day, and that its "net profit" is less than one might be led to expect from observation of the assimilation alone.

As a second example, the action of the hydrogen ion concentration of the soil may be taken. It is generally known that the p_H profoundly influences the prosperity of the plant, and that most plants can only thrive in a restricted range of p_H values. If a plant is cultured in the laboratory in a whole range of p_H values, the growth can be represented as a curve which has its optimum at a definite p_H. But this curve has little significance for the experimental ecologist. In the soil many other factors beside the p_H vary, and the proportion of mineral salts, for instance, actually influences the plant's sensibility to p_H; and according to the chemical constitution of the soil, the p_H curve assumes different forms. Without knowledge of this "*ecological* p_H curve," it cannot be asserted that one knows how the plant reacts to hydrogen ion concentration under natural conditions.

These examples, which are to be taken up in more detail, serve to illustrate the problems peculiar to experimental ecology. For the ecologist the inner mechanism of the living organism is a problem of secondary importance; he looks upon this mechanism as the weapon with which the plant has to maintain itself in the struggle for existence. Success in the

struggle is above all a question of "intensity of living," rapidity of metabolism, growth, and reproduction; and it is the aim of experimental ecology to examine the influence on these fundamental life processes of fluctuations in the plexus of external factors.

The problems of experimental ecology merge into the more practical questions of agriculture and forestry. For the agriculturalist, an exact knowledge of the natural economy of plants, on whose growth and fruiting his existence depends, is becoming indispensable. He needs to know how much nourishment is offered by the ground upon which his plants grow, and at what point artificial manuring must be applied. A rational knowledge of fertilizers can only arise as a result of a progressive ecological investigation of cultivated plants.

In conclusion, some general remarks upon the methods of research of experimental ecology will not be out of place. Without exact methods the investigator arrives nowhere; and the matter is complicated by the fact that sensitive apparatus built for laboratory use cannot be put up in the field. In order to measure ecological factors, therefore, special apparatus must be constructed, which, although built for field work, must record as accurately as possible. Since the conditions in nature are constantly varying, the instruments should be automatic, if they are to fulfil their purpose fully. We already possess automatic recording instruments for a number of factors, such as light, temperature, humidity, rain, wind, and evaporation, but a great many factors, especially soil factors, can be determined only indirectly; and there is a wide field open for scientific invention. For the precise analysis of the environment nearly all the natural sciences must be mobilized: meteorology, physics, chemistry, soil science, bacteriology, and so on. It is the lot of the biologist that he must borrow methods from all the exact sciences, or, to put it another way, —biology makes servants of all the other sciences. In any case the methods have to be adapted for biological problems.

Taking records of the environment is, however, only one of the tasks of experimental ecology. The physiological influence of the factors has also to be determined; and here again, experiments must be carried out under conditions as natural as possible. The quality of sunlight or diffuse daylight cannot be imitated. The same holds for soil conditions, for soil removed from its habitat undergoes great changes in its physical and biological condition. The essential for

successful study, therefore, is to transport the laboratory, so to speak, into the natural medium of the plant; and this can only be done by the establishment of stations in regions of ecological interest.

These, in merest outline, are the problems of experimental ecology.   It is to be the aim of the following chapters in some detail to elaborate this outline.

CHAPTER II

THE LIGHT FACTOR

1. The Light Climate of the Earth

Light is the primary factor in photosynthesis; and photo-synthesis is the most important nutritional process of the plant. It is evident, therefore, that light has a very profound ecological importance. The study of light as an ecological factor is complicated by the fact that the sun emits not only the light rays used for assimilation, but in addition heat rays and ultra-violet rays, both of which influence many other processes in the plant. In studying the influence of light, therefore, the different parts of the spectrum must be con-sidered separately. The following table gives some idea of the action of different parts of the spectrum upon the living plant:

Table I

Radiation.	Wave Length (in μ).	Action on the Plant.
Röntgen .	0·00001–0·00018	Extremely harmful
Ultra-violet	0·012–0·40	Very harmful in large quantity
Violet .	}0·40–0·49	Phototropism, morphological effects
Blue . .		
Green-red .	0·49–0·76	Photosynthesis
Infra-red .	0·76–*circa* 600	Temperature effects
Electric rays	2 mm. to indefinite	Not certainly known

Generally speaking, there exists no sharply defined distinc-tion between the action of the different rays. All rays that the plant absorbs exert a definite heat effect. Yellow and red rays are phototropically active, though to a much smaller degree than the blue-violet rays (Blaauw, 1908). The effective parts of the spectrum are usually sharply enough defined, however, to justify the use of limited spectral regions for experiments. In ecology it is sufficient for most purposes to consider, beside the total radiation, the blue-violet and the yellow-red regions separately.

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A number of methods are in use for the measurement of total radiation of the sun; one of the best instruments is the so-called pyroheliometer constructed by K. Ångström (1899). In this apparatus two similar blackened manganin strips are so mounted beside each other that alternately one or the other can be exposed to the radiation.   One strip is exposed to the solar radiation, and an electric current is passed through the other until both are receiving the same amount of heat.   The equality of heat in the two strips is verified by the aid of a small thermo-element, fixed to the under side of the strips. If the area, resistance, and absorption coefficient of the strips are known, the amount of current needed to heat the shaded strip gives a measure of the radiation, in Calories per unit time.   (*See also* A. Ångström, 1928.)

Since 80 per cent of the total energy of sunlight consists of infra-red rays, the thermal radiation of the sun can be conveniently measured with a pyroheliometer.   The values obtained, naturally, vary according to the time of year, the time of day, and the region in which the measurements are made.   The greatest intensity measured on the earth's surface is 1·64 Calories per minute per square centimetre, and this value has been recorded at Teneriffe, at a height of 3,683 metres, and at Mount Whitney in California, at a height of 4,420 metres (Dorno, 1919).   As a result of the absorption of heat by the atmosphere the intensity of radiation increases with altitude above sea-level.   Simultaneous measurements made at Teneriffe, at different altitudes, show at 80° elevation of the sun, an intensity of 1·17 Calories at 3,683 metres above sea-level, while the intensity at 350 metres is almost unity. From the values obtained at different elevations of the sun can be calculated the amount of absorption by the atmosphere, and in this way some idea can be obtained of the intensity of sunlight before it enters the atmosphere.   The value of this *solar constant*, as it is called, obtained as a mean of over one hundred measurements, is 1·925 Calories per minute per square centimetre.   Dorno (loc. cit.) summarizes the observations and calculations of radiation loss through the atmosphere in the following words: "From the total energy which the sun radiates upon the Earth, only 75 per cent reaches a height above sea-level of 1,800 metres, and, according to the number of clouds, only between 24 and 50 per cent reaches sea-level. On the average, then, the land at sea-level obtains through direct sunlight only half the radiation recorded at 1,800 metres."

Under the most favourable conditions, then, a considerable portion of the sun's radiation is absorbed by the atmosphere. Furthermore, different wave lengths behave differently in this respect. In order to discover the selective absorption of the atmosphere, the distribution of energy in the solar spectrum must be determined. An ingenious method, which has subsequently been elaborated by Abbott, was devised by the American worker Langley (1881. *See* Baly, 1927, Vol. I, p. 222). In outline, the method is as follows:

A very thin strip of platinum, blackened in camphor, is moved slowly across a spectrum thrown through a prism. The dimensions of the platinum strip do not exceed 12 mm. in length, 0·06 mm. in width, and 0·005 mm. in thickness. Through the strip runs a weak current, which can be measured by a delicate galvanometer. In its passage through the spectrum the platinum strip is heated to different degrees
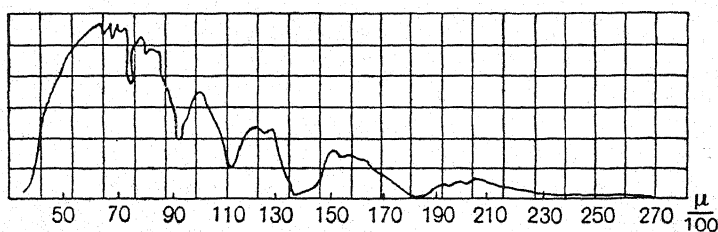

FIG. 1.—The distribution of energy in the normal spectrum at the Earth's surface. (After Dorno.)

according to the energy content of the different wave lengths, and the consequent changes in electrical resistance are measured by a continuous photographic record of the galvanometer readings. In this way a picture of the energy distribution of the normal spectrum is obtained (Fig. 1). From a number of such curves of the solar spectrum, made on clear days, and at different altitudes of the sun, the transmission coefficient of the atmosphere for different wave lengths is ascertained, and from the data, the extra-terrestrial curve of radiant energy can be calculated. The maximum energy region lies at about 0·47 μ and the curve falls from this point toward the short wave lengths more rapidly than toward the long. In the terrestrial spectrum, measured at the Earth's surface, the maximum lies somewhat toward the red end, and the sun seems yellower in colour. The drop toward the short wave lengths is steeper, since the atmosphere absorbs more ultra-violet than yellow or red. As the sun sinks, therefore, the

light becomes redder.   This definite change in colour of the sun at different altitudes is naturally of ecological significance, since photosynthesis depends principally upon the red-yellow part of the spectrum.   The relatively small amount of absorption of this part of the spectrum by the atmosphere is of considerable advantage for plant life.

Continuous measurements on a pyroheliometer will give a reliable picture of the range of solar radiation.   In the following table, taken from Dorno (loc. cit., 1919) are given the mean daily "heat integrals" for a number of regions.   The results are given in kilogram Calories.

TABLE II

DAILY TOTAL RADIATION IN CALORIES

Latitude.	Washington, 38° 93′ N.	Davos, 46° 48′ N.	Stockholm, 59° 20′ N.	Spitzbergen, 79° 55′ N.
Winter . . .	10·01	7·5	1·28	0·0
Spring . . .	24·59	22·8	17·73	6·6
Summer . . .	31·12	32·0	30·39	9·1
Autumn . . .	17·51	15·7	5·95	1·2
Year . . .	83·23	78·0	55·35	16·9

It will be observed that with increasing latitude the yearly total radiation decreases.   Moreover, the seasons themselves exhibit differences, since in the north the low elevation of the sun is compensated by the longer summer days.   Hence the total radiation in summer is about the same in Stockholm as it is in Washington, although spread out over a longer period of time.   In more northerly regions, therefore, since the total radiation of the year is concentrated largely into one season, those plants are at an advantage which possess a short vegetative period.   In the more southerly regions, whose light is equally distributed throughout the year, the developmental period is less sharply defined.   It must be left an open question to what extent light radiation, and to what extent temperature, is the deciding factor.

The light rays effective in photosynthesis and in growth processes can be measured by either photographic or photometric methods.   The photographic method is the most convenient and the cheapest, though it is less accurate.   It depends on the estimation of the time taken for a strip of light-sensitive paper to reach a definite shade, on the assump-

tion that intensity and time of exposure are constant. In the simple "normal colour photometer" of Wiesner (1907; Rübel, 1928), a strip of silver chloride paper is exposed to the light until it reaches the same intensity of colour as the standard which is beside it. The "graukeilphotometer," described by Hecht (1918; and Oberdörfer, 1928, a), operates on the same principle, and in addition can be used for the determination of total radiation over longer periods of time. Photometers requiring the use of photographic paper, have the disadvantage that only relatively high light intensities can be measured. Furthermore, normal photographic paper has its maximum sensitivity at the violet end of the spectrum. By interposing a filter the violet rays can be cut out, but the paper is so slow in reacting to the red and yellow rays that long exposure times are necessary. The "Imperial exposure meter" paper has a very high colour sensitivity. Gaslight paper can also be used, though it is not sufficiently sensitive for most measurements. Since the direction in which the rays fall upon the paper influences the degree of darkening, the intensities of direct sunlight and diffuse light cannot be compared, without the use of an opal glass filter to "spread" the light. When light of widely differing intensities is to be measured, it is best to employ a paper requiring development, a bromide paper, for instance. With such a method, the time of exposure can be kept constant, and varying intensities can be compared. An apparatus built on this principle is illustrated in Plate I a (Lundegårdh, 1923, d).

The range of the photographic methods can be determined from Bunsen's formula:

$S = i \times t$, where S is the degree of darkening of the paper, i the intensity of light, and t the time of exposure to light.

The work of Schwartzchild and others has shown that this theoretical formula can be replaced in practice by the approximation:

$E = i^q.t$; the exponent q is constant for the type of plate used. For ordinary dry plates the values lie between 0·7 and 0·8 (Dobson et al., 1926). The error involved when q is neglected is reduced if the "graukeil" type of photometer is used, for then the values depend upon the transparency of the glass wedge used.

All photometric methods depending on photography are faulty in that they require a subjective comparison of degrees of darkening. Photometers by which the intensity of light

is compared directly with that of a standard electric lamp (the "lumeter," the Macbeth illuminometer) are open to the same criticism. In fact, the only trustworthy methods are those in which the intensity of the light is measured by some physical means. The bolometer will give very accurate results when used with a sensitive galvanometer; but it gives very small galvanometer readings in the short wave region of the spectrum, and there is some difficulty in obtaining suitable filters. The bolometer is most useful to measure total radiation.

More recently Elster and Geitel (Geitel, 1920) have obtained excellent measurements of the intensity of daylight with photo-electric cells. Their method will be of great value in biology, and a brief description of it is given here.
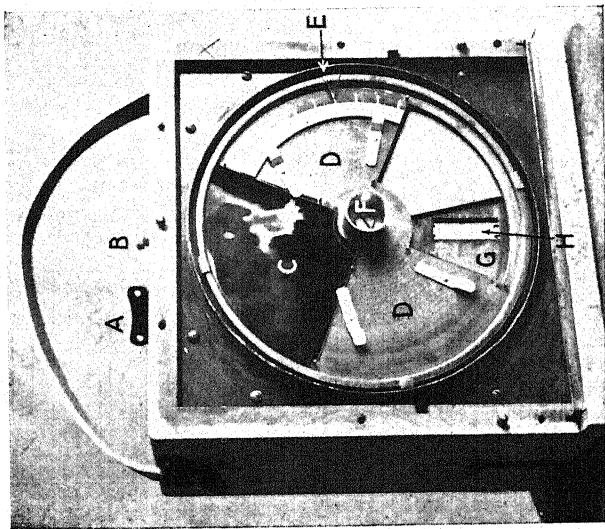
The photo-electric cell consists of an evacuated sphere of "uviol glass" or quartz. One half of the sphere is coated on the inside with a layer of metallic rubidium, potassium, sodium, or cadmium. When the sphere is illuminated, the metal emits electrons, and therefore becomes positively charged; and, over a wide range of values, the charge is proportional to the intensity of illumination. The photo-electric current is measured with an electrometer, or is amplified and measured with a galvanometer.

One of the properties of these electric cells is their selective sensitiveness, which facilitates the measurement of specific parts of the spectrum. By the use of colour filters (from Schott in Jena) the unwanted parts of the spectrum can be excluded. The region of maximal sensitiveness of different cells is as follows:
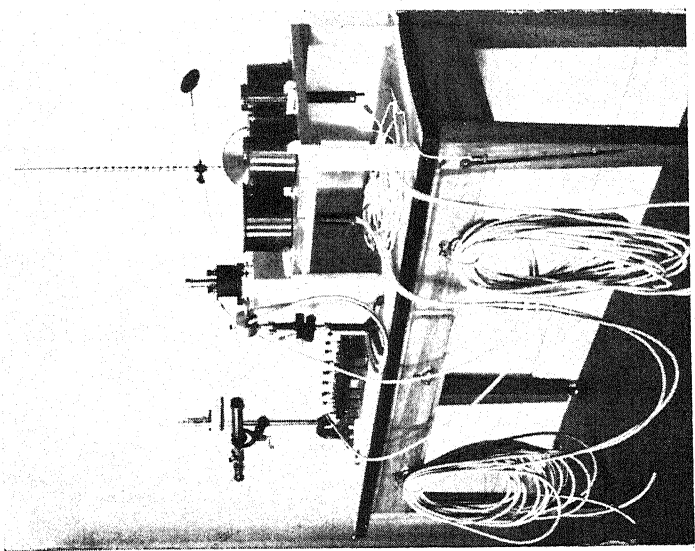
Caesium,   *circa* 5,400 Ångström units
Rubidium,   ,, 4,700   ,,   ,,
Potassium, ,, 4,400   ,,   ,,
Sodium,   ,, 3,400   ,,   ,,

Cadmium cells are not sensitive to wave lengths over 3,900, so that they can be used without colour filters for the measurement of ultra-violet radiation. The sensitiveness of the cells is increased a hundredfold if the sphere is filled with argon or helium at a low pressure.

The complication of the apparatus is apt to be somewhat disconcerting to the biologist, but its advantages are obvious. The necessary equipment for the apparatus is illustrated in Plate I *b*. When it is not required to measure ultra-violet radiation, two cells will suffice, rubidium or caesium for the yellow region, and potassium for the blue. The whole

PLATE I

(b) Apparatus for measuring illumination by means of photo-electric cells. For description see text.

(a) Apparatus for measuring the course of daily illumination (Lundegårdh). The cover has been removed. D is a disc rotating on the axis F, with a time of rotation of fifteen minutes. The sector apertures C and G are regulated by the pointer E. Over the aperture C is a yellow filter, so that the apparatus registers full light through G and the red-yellow rays through C. At H, under an opal glass film, is light-sensitive paper which moves across the aperture by clockwork.

apparatus can be carried about quite conveniently, and the galvanometer can be set up in a tent or in the open air. The cells are enclosed in a blackened metal capsule which has an opening for the various screens. The mirror galvanometer can be read with a telescope, or continuous records can be taken photographically. There is one difficulty common to all measurements of radiation, namely, that there exists no generally satisfactory unit of radiation. The total radiation is expressed usually in Calories, and the illumination is expressed in photometric units, such as lux or foot candles.[1]

At Davos, with a high elevation of the sun, the absolute brightness reaches about 216,500 metre-Heffner-candles.[1] The daily maximum does not occur exactly at midday, but some time between eleven and one o'clock, for all parts of the spectrum. At this time of the day the intensity of sunlight does not alter much, although a small depression at midday is often observed in the summer. This depression occurs in the long rays more than in the short rays of the spectrum, and it is caused by the increased vapour content of the atmosphere during the hot part of the day. In Table III are given a number of measurements of the relative light intensity on clear summer days at Abisko, in Swedish Lappland, and in Visby. It is evident that the radiation is shifted toward the red end of the spectrum in the evenings. The measurements were made with a photo-electric cell.

TABLE III

TAKEN AT ABISKO, JULY 17, 1927, AND AT VISBY, AUGUST 8, 1927. EXPRESSED AS PERCENTAGES OF THE HIGHEST TOTAL LIGHT INTENSITY AT VISBY

	12 midday.	2 p.m.	4 p.m.	6 p.m.	8 p.m.	
		Total Daylight				
Abisko	109·8	88·5	63·1	40·2	9·7	red
Visby	95·9	94·3	59·8	24·6	0·0	
Abisko	95·7	89·3	63·1	36·5	5·0	yellow
Visby	100·0	81·9	59·3	20·6	0·0	
Abisko	90·0	81·8	59·1	34·1	11·8	blue
Visby	96·4	83·2	56·8	14·5	0·0	
		Diffuse Daylight				
Abisko	13·1	9·0	6·6	4·1	2·5	red
Visby	7·4	6·6	7·4	6·6	0·0	
Abisko	14·4	15·9	11·9	9·4	6·6	yellow
Visby	16·2	15·9	14·4	10·0	0·0	
Abisko	16·8	18·5	15·8	12·5	7·4	blue
Visby	21·3	16·8	14·5	9·0	0·0	

[1] See Appendix to Chapter, page 63.

The energy content of the different parts of the spectrum changes markedly from winter to summer; in the infra-red it is increased 10 per cent, in the red 45 per cent, in the green 90 per cent, while the blue-violet is increased 250 per cent, and the ultra-violet 1,000 per cent. Consequently the composition of the solar spectrum undergoes marked changes throughout the year. Spring and autumn sunshine are markedly different, since the latter is much richer in ultra-violet rays. Infra-red radiations reach a maximum in spring, and a minimum in winter, corresponding to the humidity of the atmosphere. These results are illustrated in Figure 2. The figure also reveals the fact that the course of the curve
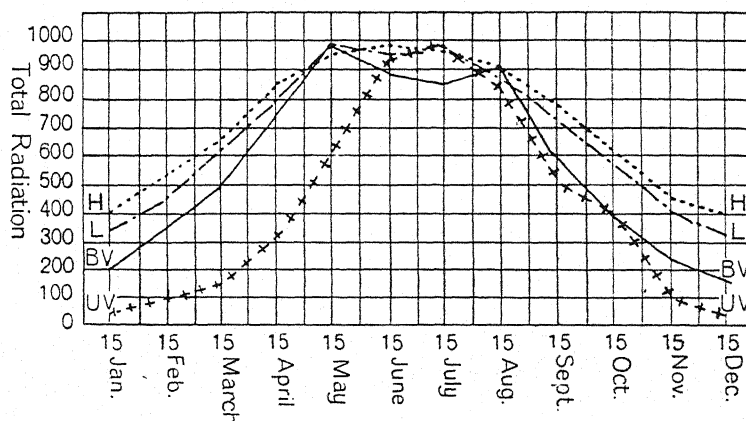

FIG. 2.—Distribution of Solar Radiation throughout the Year.

H = heat radiation.
L = visible radiation.
BV = blue-violet radiation.
UV = ultra-violet radiation.

(After Dorno.)

for ultra-violet differs from those of the other colours through September and October. Data for the yearly variation of the total energy spectrum for the latitude of Stockholm have been given by Ångström (1928).

Up to the present, consideration has been confined to sunlight itself. A certain proportion of the solar radiation as it enters the atmosphere is scattered into diffuse light, which can reach a considerable intensity, and at all events is of great importance for the ecologist. At midday in diffuse daylight, a horizontal surface receives an intensity of light fully 25 per cent of the intensity of direct sunlight, and on a clear summer day diffused heat rays may form as much as one-eighth to one-third of the total radiation. The intensity

of diffuse light from a clear sky, considered apart from the sun itself, is constantly changing in the lowlands, owing to the fluctuating moisture content of the atmosphere. In the Alps the intensity of diffuse light is much more nearly constant, but is at the same time much weaker, on account of the thinner atmosphere ; and for this reason the sky looks darker in the mountains than in the lowlands.

Clouds are of great importance for the illumination of the Earth's surface. Cirrostratus which occur grouped round the sun without covering it, can actually increase the total brightness. White clouds behave as great reflectors, but grey rain clouds diminish the total illumination considerably (Fig. 3). Furthermore, clouds affect not only the total illumination of
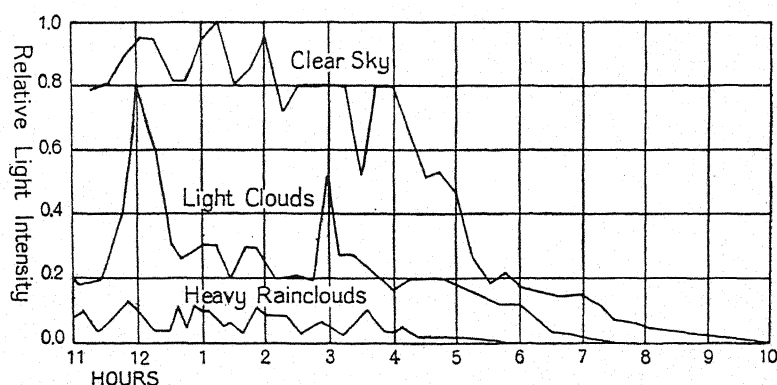

FIG. 3.—Illumination throughout the day under various conditions of clouding. (After Lundegårdh.)

the sky, but also the spectral composition of the light. According to Dorno (loc. cit.) it can be said that in general the short wave radiations are affected by clouds more than the long wave radiations are, with the exception of the infra-red.

Generally speaking, in the same latitude in Europe, the western regions differ from the eastern by a greater amount of clouding, and by a shorter mean duration of sunshine. (*See* Fig. 4.)

An alpine climate is distinguished from a lowland climate by a greater degree of clouding, and by more mist in summer. According to Hann's calculations, the Swiss plains in summer have a degree of clouding of 5·2 (10 = maximum), while values of 6·5–7·3 were reached on the peaks Säntis and Sonnenblick (taken from Schröter, 1923). The number of misty days varied from 131–226 on the peaks, and reached
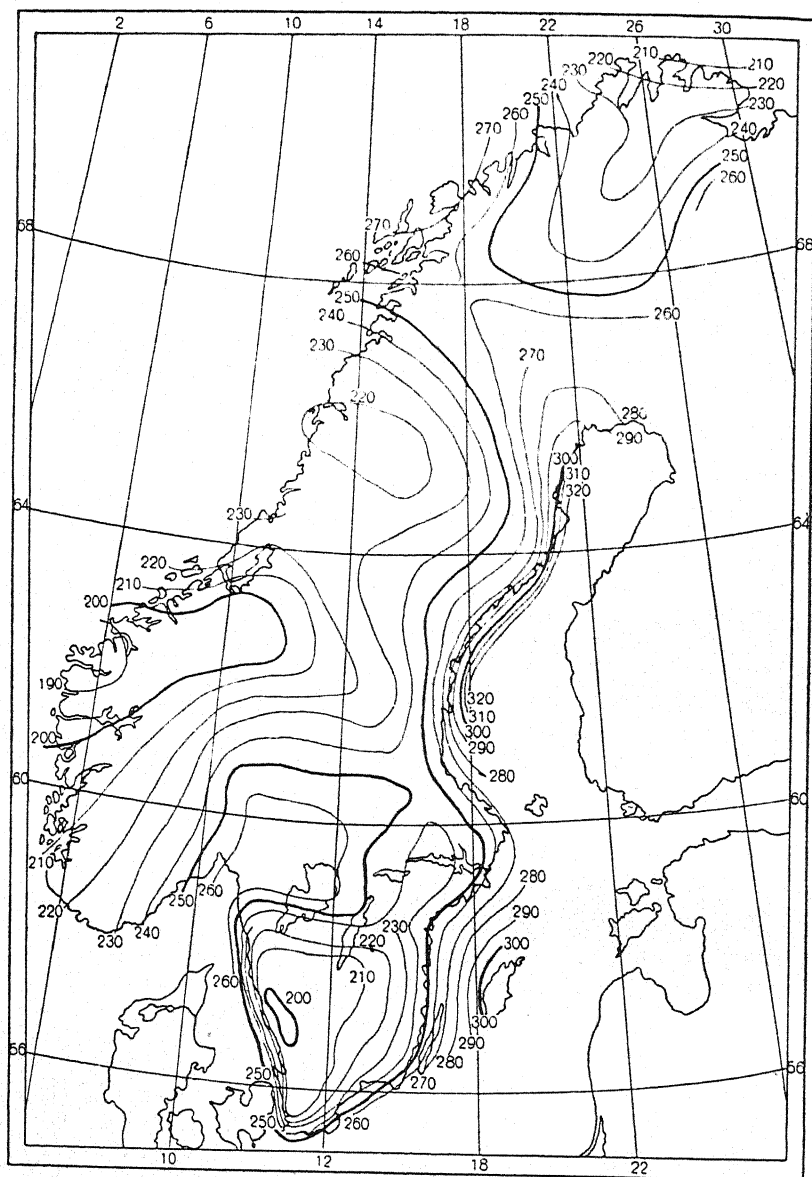
FIG. 4.—Number of hours of Sunshine in July in Scandinavia, taken from the averages from 1880–1905. (After Hamberg.)

only 44 in the plains. In the winter, on the other hand, the alpine climate is clearer than that of the lowland.

As the following figures of S. Arrhenius (1896) show, there is a zonal distribution of clouds over the Earth:

Latitude.

N													S
70°	60°	50°	40°	30°	20°	10°	Eq.	10°	20°	30°	40°	50°	60°

Mean clouding.

| 59 | 61 | 48 | 49 | 42 | 40 | 50 | 58 | 57 | 48 | 46 | 56 | 66 | 75 |

The layer of clouds over the equator seems to be very considerable; according to Hann, it reaches even 70 to 80 per cent. Consequently the illumination at the equator is less than might generally be supposed. Sub-tropical zones and the Mediterranean regions are, on the other hand, very clear and free from clouds.

2. THE ACTION OF VISIBLE RADIATION

Growth, differentiation and tropic movements are influenced chiefly by the blue-violet and ultra-violet rays. This sensitiveness to the blue-violet part of the spectrum has only been proved for phototropic reactions (Blaauw, 1908). It is common to read in the literature of "the influence of light on germination" and "the effect of light on growth" without any question being raised as to the quality of the effective rays.

Light has a twofold influence upon growth. One part of the spectrum provides the energy for carbon assimilation, and hence for the production of raw material; while another part acts as a stimulus, and influences directly the rate of growth and differentiation. Even the form of the plant is determined to a certain degree by light.

We are indebted to Klebs (1916–17) for some interesting work on the action of different regions of the spectrum upon the development of fern prothallia. He finds that red rays are most active in promoting the increase in length of the germ cells, while blue-violet rays further transverse and longitudinal division; which latter process is also favoured by carbon assimilation. It is Klebs' opinion that the growth form of prothallia depends in the first place upon the "tropic" action of light.

No very conclusive work has been carried out upon the influence of light on differentiation in higher plants. Popp (1926) and Pfeiffer (1928) have reported experiments upon the

action of different regions of the spectrum upon plant struc-
ture; and the work of Bonnier and of Schanz deserve mention.
In the years 1884 to 1886 Bonnier transplanted a number of
species from the plains to the heights of the Alps and the
Pyrenees.   Up to 1919, 58 plants had survived, and showed
remarkable changes of form.   A complete Alpine habit had
been assumed by *Helianthemum vulgare*, *H. grandiflorum*,
Silene inflata, *Lotus corniculatus*, *Alchemilla vulgaris*, and others.
The metamorphosis required different periods of time.
Juniperus communis, for example, required over 25 years, while
Galium verum required from 8 to 10 years.   Furthermore, for
every species successfully transferred from the lowlands, there
seems to be an optimum altitude for the alpine form.   If
the lowland form is planted above or below this altitude,
the metamorphosis is less pronounced. (Bonnier, 1920;
Teodoresco, 1909.)

The transplanting of alpine forms to the plains yields much
less striking results; the change takes place more slowly, and
is moreover less distinct.   This would indicate that meta-
morphosis is influenced not only by the light, but by other
factors, such as temperature.   Schanz (1918, 1919, 1923)
relates the alpine habit, i.e. short internodes, compactly
arranged leaves, a wrinkled upper surface, and dark colour, to
the high intensity of ultra-violet radiation.   In the lowlands
similar metamorphoses can be produced by adding eosin to the
nutrient substratum.

Many experiments have recently been carried out to
investigate the effect of installing "vita glass" in greenhouses.
(*See* Popp, 1926, *et al.*)   This glass allows the ultra-violet
light to pass.   Tottingham (1928) found a positive action of
ultra-violet light upon the assimilation of nitrates by wheat.

In the laboratory, the action of light upon growth has been
very carefully investigated, using the coleoptile of *Avena*
(Sierp, 1918; Watt, 1923; Priestley, 1923).   It has been
shown that light decreases the length of the shoot, and shortens
the duration of the grand period of growth.   Roots, too, grow
more quickly in darkness than in light (Kny, 1902).   The
very careful observations of Blaauw (1915) upon *Phycomyces*,
have shown, too, that darkness furthers the elongation of the
hyphae.

Leaves, and other organs of limited growth, seem to behave
differently from organs of unlimited growth, such as axes
(Jost, 1923).   Within the same species shade leaves are bigger

than sun leaves, and it has been observed that the leaves in
northern regions are bigger than those in the south; a fact
which might be related to the differing light conditions.
Unfortunately our knowledge of the influence of environment
upon leaf development is very meagre indeed.   Work has,
however, been carried out upon the influence of light upon
anatomical structure, the differences between "sun" and
"shade" leaves, and the anatomical peculiarities of etiolated
plants.   It has been shown that the cells of etiolated shoots are
bigger, and that they are less firm and less differentiated than
those of normal shoots (Küster, 1916).   Moreover, chemical
differences have been found between plants which have
received different intensities of illumination (Pfeiffer, 1926).
To the subject of "sun" and "shade"-leaves reference will be
made in a subsequent paragraph.

Among those plant movements associated with light, the
tropisms of shoot and leaf will receive first consideration.
Intensive work in the last decade has shown that the kind of
phototropic reaction depends upon the amount of light.   An
organ can react positively or negatively, or it can be apparently
aphototropic (Blaauw, 1908).   *Avena* coleoptiles, for instance,
give a positive reaction with light intensities of zero to 1,000
and 500,000 to over two million M.K.S. (*see* page 63).   Be-
tween 1,000 and 500,000 M.K.S., however, there is a negative
reaction (Lundegårdh, 1922, *b*; 1926).   Furthermore, the
magnitude of the reaction depends upon the intensity of the
stimulus, a fact which is illustrated in Figure 5.   At light
intensities of 1,000 and 500,000 M.K.S. the coleoptile remains
erect; it is apparently aphototropic.   Other objects beside
Avena, the sporangiophore of *Phycomyces*, for instance, behave
in a similar fashion (Oltmanns, 1897.)

A reversion of the phototropic reaction can be brought
about in leaves, too, by raising the strength of the stimulus.
Such a readjustment has been described by the author (Lunde-
gårdh, 1916, *b*) for the phototropic leaves of maple, and by
Lämmermayr (1916) for *Castanea sativa*.   In diffuse daylight
the maple leaves are perpendicular to the direction of the light,
but when direct sunlight falls on the leaves, they adjust them-
selves until they are set at a more or less acute angle to the rays.
It can also be shown with maple leaves that the "euphoto-
metric" and "panphotometric" types of reaction described by
Wiesner (1911 and 1913) are merely a function of the light
intensity.   As a result of their sensitivity to intensity of light

the upper leaves of a maple tree lie obliquely to the direct incident light, while the more shaded leaves below are at right angles to it.   One of the most extreme instances of orientation is to be found in the so-called "compass plants" (Stahl, 1881; Karsten, 1918), the leaves of which lie at right angles to the incident light, i.e. north and south.   The leaves of *Lactuca scariola* and *Iris pseudacorus*, for example, lie generally north and south (Erman, 1926).

A number of leaves are aphotometric, but lie nevertheless horizontally in diffuse daylight.   This is the case, for example, with beech leaves which might be described as "transversally geotropic" (Lundegårdh, 1916, *b*); and in such examples the
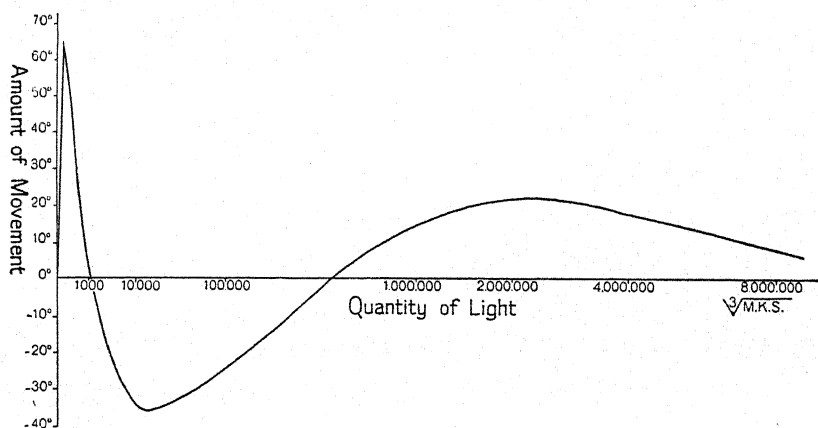

FIG. 5.—The relation between quantity of light and phototropic reaction in *Avena sativa*.   The phototropic reaction is measured as the angular deviation of the tip of the coleoptile.   (Lundegårdh, 1922, *b*.)

geotropic stimulus deputizes, as it were, for the phototropic. The same holds true for the shoot system as a whole; it is indeed usually weakly phototropic, but ordinarily it takes up its position in space wholly on account of its geotropic reaction. Only in very weak light does the phototropic stimulus dominate the geotropic (Lundegårdh, 1918).   The reaction in weak light may correspond to the first positive response represented in Figure 5, while the reaction corresponding to the second positive phase, at higher light intensity, may be much weaker.

Some plagiotropic lateral branches exhibit a very interesting adjustment to light intensity.   It has been shown (Turesson, 1919) that the horizontal shoots of the prostrate maritimal form of *Atriplex* grow upright in reduced light.   Such an adjustment is of great importance in a plant society where the

inhabitants have a struggle for space. *Galeopsis*, for example, when shaded by higher plants in a field, turns sharply upwards to grow above them. When the taller plants have flowered and died down, *Galeopsis* becomes prostrate again, spreads itself over the ground, and intercepts more light. It is clear from examples like this that phototropic phenomena have a definite ecological significance. (*See* Pringsheim, 1912.)

The way in which most germinating shoots elongate in the dark, and their marked positive phototropism, are considered to be fundamental adaptations of green plants to light. If seedlings did not exhibit these phenomena most of them would perish in the darkness of the soil. The positions of the main shoot, lateral shoots and leaves are similar fundamental adaptations to light; so also are the phenomena of phototropism in many flower stalks.

Though light certainly plays some part in the orientation of the higher plants, its influence is much more marked upon the motile green organisms. The various motile algæ have a high sensitivity to light and specific light optima, so that the depth of water at which they are found is determined by the light falling upon them.

Among higher plants, the whole arrangement of the plant body, as Sachs has pointed out (1887), can be considered as an adaptation to photosynthesis. The tropisms of the shoot, its architecture and form, the movements of the leaves, all contribute to one result—efficient carbon assimilation, which in its turn determines largely the prosperity of the whole plant. Regarded in this light, problems of leaf orientation in relation to life-forms would certainly repay investigation. As a step in this direction, Boysen-Jensen (1921), Stålfelt (1921, *b*) and Möthe (1928) have reported observations on the relationship of growth-form to the carbohydrate balance in trees.

Phototropic response of leaves to light must serve two ends. For it is of advantage for the leaf to receive as much light as possible, and at the same time to evade the heat rays falling upon it. Shade leaves arrange themselves at right angles to the strongest light, while sun leaves assume a more or less oblique position. It would obviously be disadvantageous for a shade plant, which has to "economize" with light, to possess totally aphotometric leaves.

In addition to leaf tropisms, the anatomy of some leaves is affected by light. Bright light produces thick, well-differentiated leaves, while leaves growing in shady places are thin

and poorly differentiated (Fig. 6). This plasticity in relation
to light of certain leaves must be of great value in maintaining
the efficiency of those plants on which they occur. The struc-
ture of the leaf, moreover, probably determines the shape of the
"light curve" of assimilation (Lundegårdh, 1922, *a*; 1924, *a*).
The matter receives some attention below. For various other
examples of adaptations among shade plants, for the greater
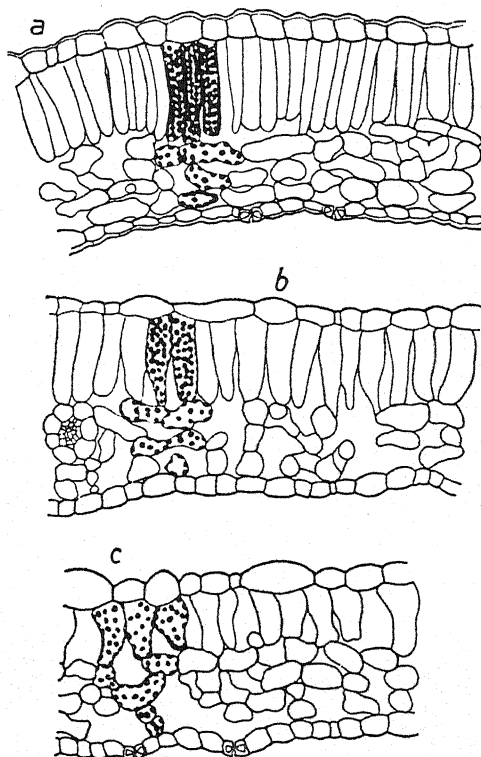efficiency in utilizing light, the reader is referred to Haberlandt

FIG. 6.—Transverse sections of *Geranium sylvaticum*. (*a*) Sun leaf, and (*b*) and (*c*)
shade leaves. (After Hesselmann, 1904.)

(1924), Morton and Gams (1925). Many plants have the
property of forming typical "shade leaves" in the shade, and
typical "sun leaves" in the sun; the beech is an example of such
a plant. The extreme shade plants, on the other hand (such as
Oxalis acetosella), are able to produce only one type of leaf
(Fig. 7); or, at best, the range of variation of leaf form is very
narrow. Hesselmann (1904) has published some interesting
work upon the plasticity of leaves to light, and to his paper the
reader is referred for further details.

Lubimenko and Forchel (1923) have investigated in a number of plants the relation between the illumination and the anatomy and chlorophyll formation. They found that on the whole, the amount of chlorophyll per unit fresh weight decreased with the illumination, while the size of the chloroplasts increased.

In conclusion, then, higher plants can be classified into those which are extreme sun plants, and form only "sun" leaves (heliophytes), (this group includes most of the maritime plants); those which are extreme shade plants, and which form only "shade" leaves (sciophytes), and thirdly, those plants which will flourish in both sun and shade, and are able to form leaves of both types.

The ecological significance of juvenile forms and adult forms presents a problem which has as yet received scant atten-
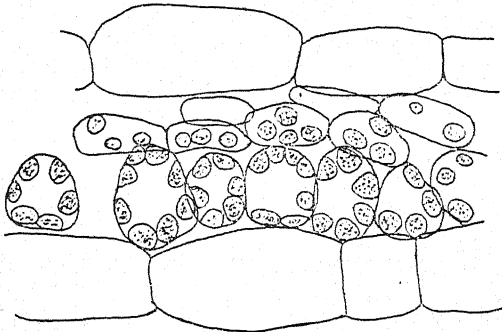

FIG. 7.—Transverse section of the leaf of *Oxalis acetosella*. (After Lundegårdh.)

tion (*see* Nordhausen, 1912). It is merely mentioned here as another of the important problems in experimental ecology awaiting the attention of the research worker.

Beside the variation of the anatomy of the leaf under different light intensities, there is the equally important variation of the chlorophyll content. In most plants the chlorophyll content varies with the light intensity. As the light intensity increases the amount of chlorophyll increases up to an optimum, above which the chlorophyll content falls again (Liro, 1908; Schmidt, 1914; Lubimenko, 1907). Among certain plants the formation of chlorophyll does not seem to depend upon light at all (Schimper, 1885), and some algæ and mosses form chlorophyll even in the dark (Dangeard, 1920; Russell, 1923). The shape and gradient of the chlorophyll-light curve is some measure of the sensitivity

to changing light intensity. In firs and pines, for example, if chlorophyll content is plotted against light intensity, when the intensity is low, the curve rises very slowly for firs and more rapidly for pines (Lubimenko, 1908; Rose, 1913; Stålfelt, 1922). From this it might be concluded that firs are better adapted to a shade life than pines. Naturally the relative chlorophyll content differs widely among different plants; and to this variation correspond differences in assimilation of the plants. Both Henrici (1927) and Stålfelt (1927) have observed periodic fluctuations in the chlorophyll content of leaves. In some South African grasses, Henrici has reported fluctuations as great as 30 per cent. Generally speaking, facultative shade plants seem to exhibit a greater plasticity of chlorophyll content than obligate shade plants.

The influence of light upon germination has obviously some ecological significance. It is well known that many seeds germinate only after they have received a certain amount of light, often a very small quantity indeed; others can germinate as well in complete darkness as in light (Lehmann, 1918; Noack, 1920; Jost, 1923); while in a third group germination is actually inhibited by light.[1] According to Baar (1912), the germination of the *Amaranthaceae* is inhibited by light. It is of interest that this sensitivity to light is influenced by both temperature and chemical stimuli. In ferns, too, all transitions are found between "light-germination" and "dark-germination"; and, according to Klebs (1917), the red rays of the spectrum promote germination, while the blue-violet rays inhibit it. The mechanism of this influence of light upon germination is not fully understood. Often the action of light can be replaced by chemical action. It cannot be decided at present, to what degree these phenomena appear in Nature, and whether the influence of light upon germination plays any part in plant distribution.

The buds of many trees are influenced by light in a way analogous to its influence upon germination. According to Jost (1894), the buds of the beech require light before they will shoot, while in other plants such as the cacti (Goebel, 1913) light has an inhibitory effect upon sprouting.

From the foregoing paragraphs it is clear that light has a most diverse influence upon development, and that, quite apart from its importance in photosynthesis, it has a profound

[1] In the dark only 7 per cent of Lythrum seeds will germinate; and an exposure to light of 73 M.K.S. will bring about a 50 per cent germination.

ecological significance of which we know very little at present.
The relative importance of the short and the long rays, as
concerns their influence upon plants, is still imperfectly
understood; but there is no doubt that the proportion of
short to long rays, which is much lower in forests than in
the open, is not without significance upon the plant life in
those situations.

Strong light is harmful to fungi and bacteria; in fact
bacteria are even killed by an excess of it (Bedford, 1927).   An
open piece of ground, therefore, flooded by the sun, cannot
shelter in its upper layers the same important population of
micro-organisms as can a shady soil in the forest.   In fact a
real mould soil, after it has been open to the light, is easily
transformed into acid humus soil, owing possibly to the
inhibition of natural decomposition (Hesselmann, 1917), and
to the changed moisture content.   Moreover, the weakening
of the ultra-violet rays in a forest must affect those higher
plants upon the floor of the forest.   Differentiation and growth
in size is favoured under these conditions, while in the open,
especially in mountains, where the blue-violet rays are strong,
there will be expected a definite stunting of growth, a condition
which has often been observed in the Alps.

In discussing the ecological significance of light, it must
be borne in mind that many of the conditions produced in the
laboratory never really occur in Nature, and therefore can play
no vital part in the life of the plant.   This is true, for example,
in the "negative reaction" phase of phototropism, which occurs
for coleoptiles of *Avena*, it will be remembered, at intensities of
between 1,000 and 500,000 M.K.S.   This negative reaction
would not occur in Nature, for even at the weakest light
intensities the length of illumination is so long that the total
amount of light would be greater than 500,000 M.K.S.
Suppose that the light intensity on the ground of a wood were
as low as 5/1,000 sunlight.   This is equivalent to 250 metre
candles, and it would fall upon the habitat for at least six hours
daily.   Even this totals to 540,000 M.K.S., a figure above the
limit of negative phototropism.   In any case, even a shade
plant like *Oxalis* would starve if it were put in so feeble a
light.

If the negative reaction ever did occur in Nature it would
be decidedly unfavourable for the plant; so that the initial
negative reaction of plants to light, which is apparently a
general phenomenon, might be regarded as one of the "unsuit-

able adaptations" of plants (Lundegårdh, 1926). There are indeed a number of plant movements which are very difficult to interpret as "advantageous" to the plant: for example, the positive phototropism of the sporangiophore of *Pilobolus*, the nyctinastic movements of leaves, and the involved movements of flowers and fruits. (*See* Goebel, 1920.)

In this connection, another fact observed above is worthy of reiteration, namely, the way in which a plant orientates itself best with regard to the light, by the means, not of phototropism, but of geotropism. And even if phototropism does come into play, the short waves effect the movement, while the *result* of the movement, which is more efficient assimilation, is concerned with the long wave-lengths. Blaauw has shown that the red rays are not completely ineffective, but that their action is 2,000–3,000 times weaker than that of the blue rays. Even in forests there is doubtless enough of the short waves to effect phototropic movements.

Of the total energy reaching the atmosphere, estimated at 1340^6 billion Calories per annum, only about one eight-thousandth, or 162^3 billion Calories are used in photosynthesis (Schroeder, 1919). Of the total visible spectrum, between 0·6 and 7·7 per cent is transformed into chemical energy in the green leaf (Puriewitsch, 1914). A small fraction of the remainder passes through the leaf, but most of it is absorbed as heat, and increases the transpiration (Willstätter u. Stoll, 1918). Different parts of the visible spectrum are used to different degrees in photosynthesis. The original investigations of Englemann and the more recent work of Kniep, Minder, Ursprung, and others (Ursprung, 1917), have shown that both the long and the short waves are photosynthetically active, but that the absolute maximum lies in the red (660–680 $\mu\mu$). Whether a secondary maximum occurs in the blue, as certain workers declare, has not been conclusively shown. At all events assimilation in the ultra-violet and the infra-red is very low indeed. Warburg (1923), using *Chlorella*, found that the greatest uptake of energy occurred in the yellow (570–645 $\mu\mu$). Fully 70 per cent of the light was used in this region. In the red region 59 per cent was utilized, and in the blue only 33·8 per cent. Comparable results have been obtained by Wurmser (1923), who used *Ulva*, and found a utilization of between 53 and 64 per cent at $\lambda = 590 \mu\mu$.

In spite of certain minor discrepancies, the researches of all workers in this field combine to show that the red end of the

visible spectrum is of primary importance for photosynthesis. It is manifestly important that this should be realized in ecological work. The measurements of light, recorded in the earlier literature, which were carried out by Wiesner's method have a very limited value, for, apart from the errors introduced by the omission of an opal glass screen, they represent only the intensity of the short wave region of the spectrum.

The only completely satisfactory method of measuring light intensity would be a spectroscopic method, whereby the energy value of each part of the spectrum would be recorded. Such an exact analysis of the light factor would need a very complicated and expensive apparatus, which unfortunately could not be carried about in the field and rapidly set up any-where.

The drawback of Weber's portable photometer, and other photometers of the same sort in which colour filters are used, is that although the readings they give may be tolerably accurate, they cannot be used for continuous records. The photo-electric cell is obviously the most satisfactory method, though it is somewhat difficult to manipulate. In ecological work, then, it is best to ascertain the general relationships of light intensity at various altitudes, at various degrees of cloud-ing, etc., with the more complex instruments; and to deter-mine the light conditions at different habitats with a continuous recording photometer (already described, p. 12) which can be set up anywhere, and which is not too elaborate. If the solar energy measured can be divided even into two regions of the spectrum, long and short wave lengths, there is a great advan-tage gained over the older methods. In comparing the illumination of two widely separated regions the results must be expressed in some absolute units. It is most desirable, of course, to express the results in energy values rather than light intensities.

For the ecological analysis of different habitats in one restricted region, such as a forest, it is sufficient to express the results on a basis of relative light values; the intensity in each habitat, for instance, can be expressed as a fraction of the simultaneously prevailing intensity in the open. For pur-poses of comparison throughout the year, the light intensity in the open of a clear day in July can be taken as standard; and this standard can at any time be turned into absolute units.

Before discussing the part which light plays in determining

a plant habitat, something must be known of the relationship between photosynthesis and light intensity. Attention will be confined here to the ecological side of the problem. The physiology of photosynthesis has been fully discussed in two recent monographs (Stiles, 1925; Spoehr, 1926).

At constant temperature, and constant concentration of carbon dioxide in the air, the curve between light intensity and photosynthesis rises at first in a straight line, then falls off gradually, until in full sunlight it is almost horizontal. The falling off in the curve occurs earlier in a typical shade leaf than in a typical sun leaf. At weak light intensities the assimilation of shade leaves is as efficient as that of sun leaves or perhaps
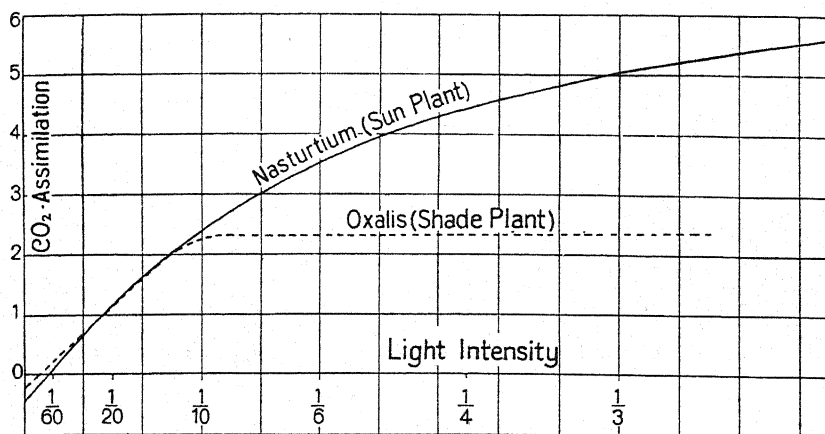

FIG. 8.—The ecological assimilation curves of sun and shade leaves. (Lundegårdh, 1921.)

even more so. But above a certain light intensity the behaviour of sun and shade leaves begins to diverge (Fig. 8), a phenomenon of obvious ecological importance. The writer has shown (1921) that the point of inflection of the curve occurs at a light intensity one-tenth of that of a clear July day, in the case of *Oxalis acetosella*, *Melandrium rubrum*, and *Circaea alpina*, which grow in the shades of woods. It was somewhat lower for *Stellaria nemorum*, and higher in the shade ferns investigated by Johansson (1923). There exist all transitions between the curve of the typical shade curve (Fig. 8) and that of the typical sun leaf. (*See* Lundegårdh, 1924, *a*.) Some of these are illustrated in Figure 9.

It has been observed that all assimilation curves rise more rapidly at lower light intensities than at higher; although they do not follow a logarithmic curve they are suggestive of such a

curve.   This is a particular instance of a more general rela-
tionship which can be expressed in the following way:

The effect of unit increase of light intensity upon assimila-
tion is greater, the nearer light approaches to a "minimum
factor."   This statement the writer proposes to call the *Law of
Relative Effects* in assimilation (Lundegårdh, 1924, *a*).[1]   By
the minimum value of the light factor, then, is understood that
intensity of light at which any change has its most profound
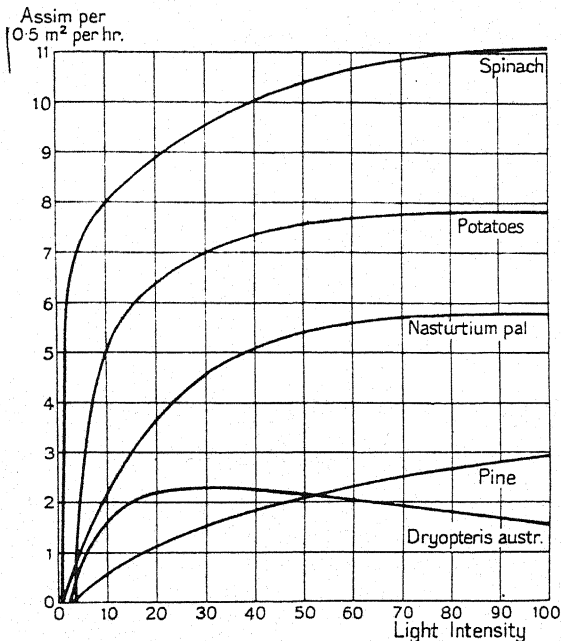effect upon assimilation.   Under natural conditions the value

FIG. 9.—The light-assimilation curves of five plants.   Curve for pine from Stålfelt,
for *Dryopteris* from Johansson, and the others from Lundegårdh.

is generally less than one-tenth of July sunlight, though in the
case of certain conifers it may be as high as one-fifth (Stålfelt,
1922).

At high intensities (1/3–1/1 July sunlight), the influence
of changes of light intensity upon assimilation are insignificant.
In shade leaves especially the effect is almost negligible; indeed
it can be even detrimental if secondary processes such as the
closing of stomata, or rise in temperature intervene (cf. curve of
Dryopteris, in Fig. 9).   In sun leaves the effect of a change in

[1] The word proposed by Lundegårdh is " Relativitätsgesetz " (Ed.).

light intensity in the maximal region differs according to the shape of the assimilation curve, though it is always much less, of course, than a similar change when light is in the minimal region.

Since the assimilation curve does not approximate to any mathematical curve, any quantitative expression of the law of relative effects must be an empirical expression. The "relative efficiency" of a factor might be expressed as $\dfrac{\Delta E}{\Delta F}$ where an increase in the factor ΔF causes a corresponding increase in the assimilation ΔE. Suppose a 10 per cent increase in the environmental factor be taken as a basis of calculation, then if E be the assimilation when the intensity of the factor is F, and E_1 the assimilation when the intensity of the factor has been raised to $F + \dfrac{F}{10}$, the relative efficiency of the factor becomes:

$$\frac{(E_1 - E)10}{E} = A.k$$

Under favourable conditions, when the factor is in the minimal region, the value for $\dfrac{E_1 - E}{E}$ is $\dfrac{1}{10}$, and A.k has the maximal value, unity. In the maximal region $\dfrac{E_1 - E}{E}$ approaches zero (i.e. the horizontal part of the curve), or it can actually assume negative values.

As far as the absolute intensity of assimilation is concerned, the optimum is markedly lower for shade leaves than for sun leaves. The assimilation per unit leaf area among the phanerogams is remarkably uniform, though there do occur marked differences among the sun leaves themselves. The order of assimilation intensity can be gathered from the figures in Table IV.

The results of many authors cannot strictly be compared with one another, for their experiments differ markedly as to temperature, carbon dioxide content, stomatal aperture and so on. Some experiments carried out by the present writer have shown an increase in the assimilation when the air around the leaves is in motion (Lundegårdh, 1928, 1921, b). The photosynthesis of leaves which assimilate slowly, however, can be measured satisfactorily in still air (Stålfelt and Johansson, 1928).

TABLE IV

THE ABSOLUTE ASSIMILATION INTENSITY, AT TEMPERATURE 18–20° C., IN THE MAXIMAL LIGHT REGION ($\frac{1}{1}$–$\frac{1}{4}$ LIGHT), AND NORMAL CO_2 CONTENT OF THE AIR (0·56 MG. PER LITRE).

Plant.	Assimilation, in mg. CO_2 per 50 cm² leaf surface per hour.	$C_6H_{12}O_6$ per sq. metre per hr. in gm.	Observer.
Potatoes . .	9·57	1·30	Lundegårdh
Tomatoes . .	8·42	1·15	,,
Sugar beets . .	9·26	1·26	,,
Spinach . . .	9·78	1·33	,,
Vicia faba . .	8·83	1·20	Walther
Phaseolus vulgaris .	9·27	1·26	Yoshii
Oxalis acetosella .	2·4	0·33	Lundegårdh
Oats . . .	max. 20 mg. per gm. fresh wt.	—	Burström (in the author's lab.)
Dryopteris austriaca	2·44 ⎫ per gm.		Johansson
Pinus sylvestris .	3·00 ⎬ fresh wt.	—	Stålfelt
Picea excelsa . .	2·00 ⎭		,,

If a method for the measurement of assimilation is to be trustworthy, the following conditions must be satisfied:

1. The concentration of carbon dioxide must be normal.
2. The leaves must be fully turgid, and have had a period of rest from assimilation, so that they contain the minimum of assimilates.
3. The stomata must be open.
4. The air around the leaves must be sufficiently in motion to prevent shortage of carbon dioxide.
5. The source of light should be daylight, or as like daylight as possible. The light of certain metal filament lamps is satisfactory in this respect.

An apparatus for measuring the assimilation of carbon dioxide, which complies with the above five conditions, is illustrated in Figure 10, and has been described by the author (Lundegårdh, 1924,*f*). The assimilation is measured by an analysis of the carbon dioxide content of the air before and after the experiment.

When higher concentrations of carbon dioxide are to be used, the apparatus can be simplified, for the movement of the air is not a factor of importance. Volumetric methods, which are unsuitable for normal concentrations of carbon

dioxide concentration, can be used when the carbon dioxide
is in maximum.

The normal concentration of carbon dioxide is suboptimal
for assimilation. When the concentration is raised to 1·22
per cent, the maximal assimilation will reach values as high
as:

40·07 mg. CO_2 per hour per 50 cm² at 30·2°C. (potato)
30·3   ,,   ,,   ,,   ,, 35·5   (tomato)
29·9   ,,   ,,   ,,   ,, 36·1   (cucumber)

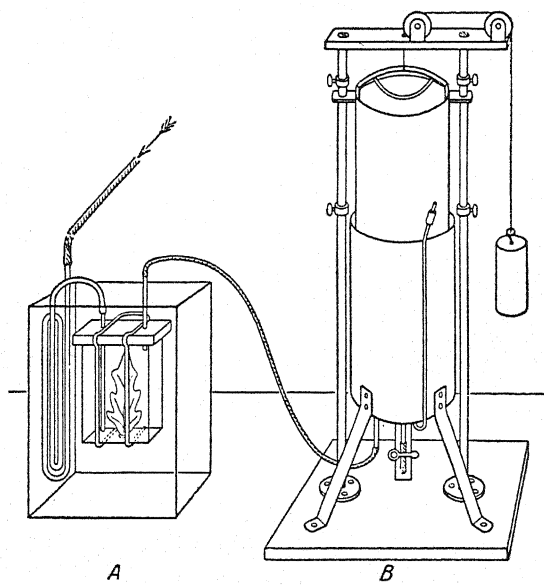It is clear that under natural conditions of carbon dioxide

FIG. 10.—Apparatus for determination of assimilation. A, assimilation chamber,
containing a leaf, immersed with a glass spiral tube in a water-bath at constant
temperature. B, for analysis of carbon dioxide, and serving also as an aspirator.
(Lundegårdh, 1924, f.)

assimilation, plants are by no means assimilating at their maxi-
mum efficiency. There is a general similarity among the sun
plants as regards assimilation intensity, while the assimilation
of conifers approaches to that of shade plants. These low
intensities of assimilation among conifers may depend partly
upon a poverty in chlorophyll content (Table V).

Emerson has recently shown that the assimilation of
Chlorella is proportional to the amount of chlorophyll
(1929). It is probable that other factors, such as the

TABLE V

THE CHLOROPHYLL CONTENT OF LEAVES, ACCORDING TO WILLSTÄTTER AND STOLL, STÅLFELT, AND LUBIMENKO

Plant.	Chlorophyll per 10 gm. Fresh Leaf.	Plant.	Chlorophyll per 10 gm. Fresh Leaf.
Acer pseudoplatanus .	40·0–49·3 mg.	*Ulmus sp.* . .	16·2 mg.
Ailanthus glandulosa	46·0 mg.	*Pinus sylvestris* .	10·9–17·8 mg.
Rubus sp. . .	32·4 ,,	*Taxus baccata* .	13·8 mg.
Zostera marina .	29·3 ,,	*Laurus nobilis* .	12·7 ,,
Tilia cordata . .	28·1 ,,	*Picea excelsa* .	10·6 ,,
Quercus robur .	25·0 ,,	*Ulva lactuca* .	6·9 ,,
Sambucus nigra .	22·7 ,,	*Padina pavonia* .	5·9 ,,
Fragaria vesca .	17·7 ,,	*Dictyota fasciola* .	2·8 ,,
Cucurbita pepo .	17·5 ,,	*Phyllophora rubens* .	2·4 ,,
Helianthus annuus .	16·5 ,,	*Laurentia coronopus* .	0·8 ,,

"protoplasmic factor," play a part too, for Willstätter and Stoll found an unexpectedly high intensity of assimilation in a form of *Chlorina* poor in chlorophyll (1918).

The flattening of the light assimilation curve at higher light intensities is not due to inability on the part of the chlorophyll to absorb and utilize light energy, but to the fact that other factors, such as carbon dioxide, "limit" the assimilation. Carbon dioxide is present in the atmosphere only in comparatively small concentration, and if an extra dosage of carbon dioxide is added to the atmosphere, the assimilation is proportionately raised (Bolas and Henderson, 1929). Assimilation is sometimes reduced because the structure of the leaf is such that the entrance of carbon dioxide is obstructed. In comparing the assimilation rates of different plants, therefore, the architecture of the leaves must be taken into account. In a thick leaf, for example, the lower chloroplasts receive much less light than those in the upper part of the leaf. Such a leaf, therefore, is not so efficient as a thin leaf of the same chlorophyll content. (*See* Stålfelt, 1924; Lundegårdh, 1922, *a*; Schroeder, 1924.)

It remains to be considered what significance the light-assimilation curve has for the experimental ecologist. There is a close relationship between the shape of the light-assimilation curve and the type of plant. It is obviously of great advantage for a sun plant to have leaves which will utilize all

D

the light, even at the highest light intensities.   Sufficient data are not available for determinations of the relative efficiency (A.k, page 30) of the light factor upon different plants, but this should be one of the ultimate aims of the ecologist. If, for example, a curve of the relative efficiency of the light factor, for successive 10 per cent increments could be plotted, it would give a complete picture of the dependence of the plant upon light as a factor in photosynthesis.

For the assessment of the real carbohydrate balance of the plant in its natural habitat, more than the light-assimilation curve is necessary.   The conditions of illumination of the habitat must also be determined.   To obtain results of any accuracy, it is insufficient to make a few measurements of light intensity, and from these to calculate a mean intensity of the habitat: for light varies enormously with time of day, time of year, and with clouding.   It is indeed quite fallacious to work with mean values of light intensity as the following example illustrates:

Given the form of the assimilation curve, and the light intensity of the habitat, it is easy to calculate the amount of carbohydrate which would be formed.   Now if the mean value of light intensity is used in such calculations, the value of the result will be too high, for it will have been tacitly assumed that a positive deviation from the mean light intensity has as great an effect as a negative deviation; and this is obviously not the case.   The error of such a method increases with the magnitude of the diurnal fluctuations in light intensity.

In order to determine with any accuracy the conditions of illumination in a habitat, observations must be taken at short intervals, and from the assimilation-light curve the corresponding rate of photosynthesis for each interval can be determined; and by the summation of these successive rates the gross daily assimilation can be calculated.   Reliable results can be obtained with successive intervals of a quarter of an hour to an hour, and to take readings at smaller intervals of time would scarcely be practicable.   Methods of this sort will disclose distinctions which would not be disclosed by the methods using mean daily light intensities as a measure. Two habitats, for instance, might have exactly the same mean light intensity, but the light in one might vary markedly throughout the day, and consequently be of less use in assimilation than the light in the other where the diurnal illumination is more equable.

In estimating the importance of calculated assimilation values it should be remembered that, despite its importance, light is only one of a host of factors affecting assimilation. Temperature, concentration of CO_2, the condition of the stomata—all these factors must be as closely studied as light, and eventually their interaction must be understood.

In suing data for the assimilation of cut leaves for an understanding of the photosynthesis in the living plant there must be no doubt that the cutting of the leaf has not disturbed its assimilation. It has been established that photosynthesis itself is not affected; but it cannot be assumed that the turgor and the stomatal aperture remain unchanged. By careful manipulation, however, this difficulty can be overcome. Maximov (1928) reported wide fluctuations in the assimilation of cut leaves over short periods. Beljakoff, working in the writer's laboratory, has shown that these fluctuations can be attributed to faults in the method. In oats and beans Beljakoff found remarkably constant values of assimilation for an hour after cutting and illuminating the leaf.

Great restraint is always necessary in applying the results of laboratory experiments to ecological problems. The most accurate determinations of the light factor will give only an "ideal" assimilation value. It is impracticable at present to estimate the daily income and expenditure of a plant, though the assimilation and respiration provide a satisfactory first approximation.

In recent years many attempts have been made to follow the assimilation of plants in their natural habitats. Curves of CO_2 absorption through the day have been made by F. McLean (1920), Kostytschew (1926, a; 1926, b; 1928) and Zemkuznikow (1927); and the formation of starch throughout the day has been followed by Thoday (1910), Stănescu (1927), Langner (1927) and Kokin (1928). Thoday and McLean found that on warm dry days scarcely any assimilation occurred at midday. This saddle-shaped depression in the diurnal curve depends probably upon a closing of the stomata, and an accumulation of assimilates.

The "ideal" curves of assimilation obtained in the laboratory are valuable in that they give some idea of the "ecological amplitude" of the plant. The essential difference between sun and shade leaves, for example, is admirably demonstrated by their respective "ideal" assimilation curves.

3. Light Climates in Geographical Regions

The early measurements of light intensity made by Wiesner, Hesselmann, Rübel, and others, using a simple photographic method, admit, in spite of the shortcomings of this method, of certain general conclusions with regard
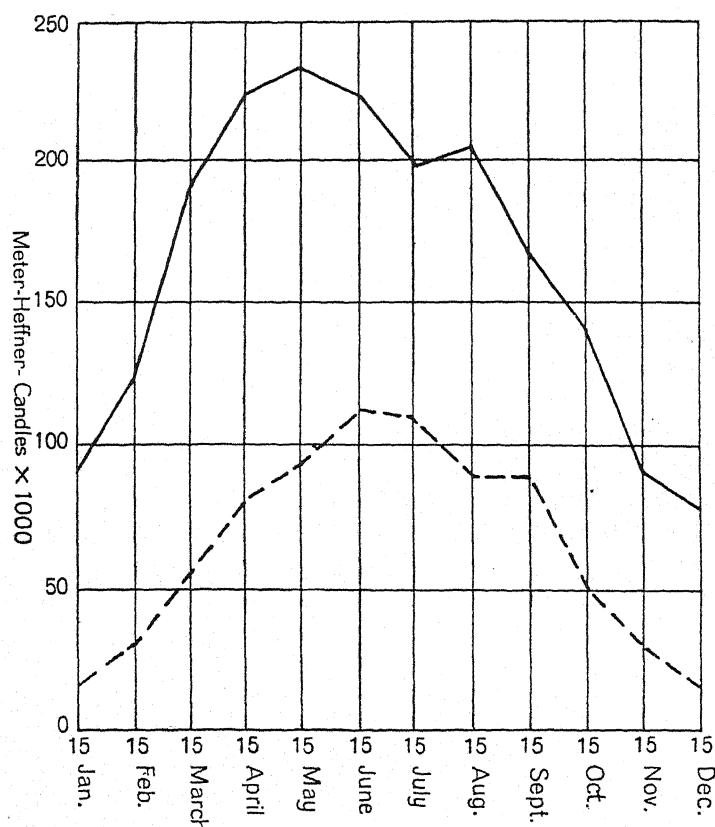
Fig. 11.—Light intensity at midday from Davos (upper curve) and Kiel (lower curve); monthly means, by Weber's photometric method 1908–10. (After Schröter, 1923.)

to the differences in light climate in the lowlands, in the Arctic, in mountains, deserts, upon the sea, and so forth.

Rübel (1908) measured at the St. Bernard, in the Alps, at a height of 2,309 metres, a maximal total intensity of 1,800 Bunsen units against 1,500 Bunsen units in Vienna, as recorded by Wiesner. In a balloon at 4,200 metres an intensity of 2,304 units has been recorded; according to Schröter, the intensity rises 45 per cent for every thousand

metres (Dorno, 1919). Dorno (loc. cit.) has shown by more modern methods that the intensity of illumination at Davos is 1·8 times that in Kiel in the summer, and fully six times that at Kiel in the winter (Fig. 11). Even taking into account the difference in latitude of the two places, conditions of illumination in the mountains are far superior to those in the plains, especially in the winter time. Now it is significant that the superior illumination of the Alpine climate depends almost exclusively upon the direct sunlight. Under normal conditions the diffuse light of the white-blue sky in the plains is much brighter than diffuse light in the Alps, often reaching twice the value of the latter. On account of this, shade plants are said to thrive much better in the plains than in the Alps. (*See* Schröter, 1923.)

The illumination of a habitat is greatly increased by the presence of snow. A snowfield with a slightly frozen surface reflects back almost 89 per cent of the light falling upon it; plants which can still assimilate at the low temperature of a snowfield receive, therefore, an extraordinarily intense illumination (Henrici, 1921, *a*). The additional interesting observation was made by Henrici (1918) that the assimilation of plants receiving light from the snow is subnormal, a fact which she traced to the poverty of red rays. According to this author, Alpine plants are all adapted to the powerful light of mountain regions. *Anthyllis vulneraria, Bellis perennis, Primula farinosa,* and *Taraxacum officinale* have all been investigated, and it has been found that their compensation points are higher than those of the same species dwelling in the plains.

Another remarkable fact observed by Henrici is that the Alpine forms contain significantly less chlorophyll than the lowland forms. The only exception is that plants dwelling in snow valleys build up more chlorophyll. These examples ~:om the Alpine flora confirm the general hypothesis that the :mount of chlorophyll is in an inverse proportion to the intensity of the illumination. In accordance with Stahl's suggestion (1908) this phenomenon might be interpreted as a protective adaptation against too strong an absorption of light. A surface poor in chlorophyll reflects and transmits more light than a surface rich in chlorophyll; and would therefore be less strongly heated by a powerful illumination, and incidentally would absorb less ultra-violet radiation. Work upon the assimilation of ultra-violet rays has been

carried out by Ursprung and Blum (1917) and other workers, and these workers have found that the outer wall of the epidermis, and especially the cuticle, protects the plant against these short waves. Müller (1916) reports that certain liverworts are protected against the intense light in the Alps, by a red coloration or by the formation of air chambers.

Since direct sunlight is richer in red rays than diffuse daylight, Alpine plants receive radiation much more efficient for photosynthesis than do lowland plants.

As in the Alps, so in the desert, there is a reduction of the proportion of diffuse daylight. Rübel (1910) has found that on the high northern edge of the Sahara, direct light is from twice to eight times the intensity of diffuse light; and on the peak of Mount Atlas (2,060 metres) 3·5 times that of the diffuse light. This weakening of the diffuse light, and hence of the whole light climate, depends probably upon the dust in the desert air. After prolonged rain, the total illumination of the desert is significantly enhanced.

Diffuse daylight reaches its maximum in the dust-free coastal regions of the lowlands, and here a rich "shade flora" is developed at its best. Diffuse light is particularly strong owing to the fact that the sky is frequently over-clouded. When the sun reaches an elevation of 16° at St. Bernard, the ratio of sunlight to diffuse light is unity. In Lisbon and Vienna the ratio does not become unity until the sun has an elevation of 51° to 60°.

Even when the sun is under the horizon, as in Arctic and sub-Arctic regions, the illumination due to diffuse light can be considerable. Kostytschew (1921, *b*) has examined the efficacy of this light in assimilation. In Petrograd (60° N.) photosynthesis was suspended after sunset in *Alnus incana*, *Betula verrucosa*, *Lamium album*, *Dactylis glomerata*, etc. This cessation of photosynthesis Kostytschew attributes to the closing of the stomata. It would seem that the plant is living below its compensation point, for carbon dioxide is often given out. On the contrary, *Pinus Strobus* and *Abies Sibirica* exhibit positive assimilation all the time. According to Müller, *Chamaenerium* in Greenland, at midnight, and at a temperature below 10° C., will show a slight positive assimilation (1928). In the summer, plants in sub-Arctic regions receive more light than those farther south. In Godhavn (69° N.) at midnight, there is about the same

light intensity as is found in a thick wood in Denmark at midday (Müller, 1928; Lundegårdh, 1928).

It is remarkable how much light a plant may receive by reflection from the ground or the sea. A considerable amount of light is reflected from the sea, which is undoubtedly of advantage for adjacent littoral forests. A psammophilous flora can receive from 10 to 20 per cent of its total illumination from the sand below it. Even in a cultivated field the light reflected from below can be a significant factor,
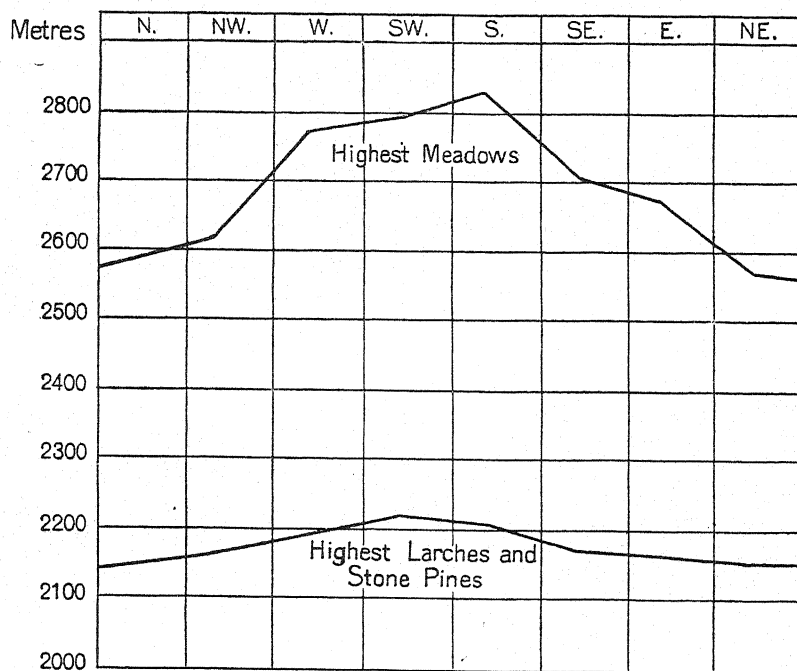

FIG. 12.—Highest occurrence of pasture and of trees in the Adamello group.
(Schröter, 1923.)

depending, of course, upon the amount of vegetation in the field. C. Shull (1929) has worked upon the reflection of light from leaves, and has found that a considerable amount of light can be so reflected. (*See also* McLean, 1919.)

The ecological effect of light in open habitats must not be overrated. A high mean light climate is effective only in the morning and the evening, when light is a minimum among the plexus of factors acting upon the plant. At midday light is in its maximum region, and it may fluctuate within wide limits without affecting the assimilation of the

plant. In a shade flora, where the light factor is continually
in a minimum, differences in the light climate show their
most marked effects.

The higher the proportion of sunlight to diffuse light,
the more marked are the differences between the north,
south, east and west exposures of a habitat. According to
Rübel, the south side of a mountain is $5\frac{1}{2}$ times as strongly
illuminated as the north side. It is not therefore surprising
that the altitude to which a particular species will climb
depends markedly upon the exposure upon which it is
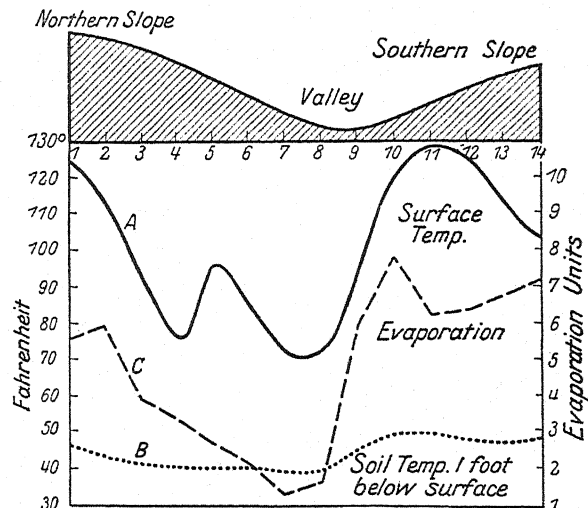
FIG. 13.—Section of the "micro-climate," in a valley running east to west in the
Rocky Mountains (Colorado). The curves show the influence of the direction
which the habitat faces upon the surface temperature and the evaporation.
(After Braun-Blanquet, 1928.)

growing. Schröter has shown that the tree line in Switzer-
land may vary within 300 feet, according to the exposure
(1923), while, according to de Candolle, the mean altitude
of the same species growing on a southern and northern
exposure may differ by 200–300 metres. The greater the
altitude, the more striking is the contrast between northern
and southern slopes (Fig. 12). The determining factor in
the exposure is probably the radiation of heat from the
sun; the temperature of the soil depends to a great extent
upon insolation (Fig. 13). Since the relative intensity of
vertical to lateral illumination increases with increasing
latitude, the direction which a habitat faces becomes of
greater importance as one proceeds northwards.

Even on the north and south sides of individual trees there have been observed differences of vegetation; but although this fact has been used by scouts and American Indians for years, it has never been thoroughly analysed.

In the Arctic, conditions of illumination are in many ways peculiar. Diffuse light forms a large proportion of the total illumination, and the apportionment of light throughout the year is very different from that in southern latitudes. Our knowledge of the conditions of illumination in the Arctic is very imperfect, though Wiesner (1907) has published some observations upon this subject. He has recorded that the relative "light requirements" of plants increase with the latitude. The "Lichtgenuss" for *Betula nana*, for instance, amounted to 1–1/3·4 in Oslo, 1–1/2·2 in Tromsö, and unity in Spitzbergen. Without knowledge of the absolute light intensities, it could not be decided whether plants in the north really required a higher light intensity than those in the south. It might be imagined, on the contrary, that since they receive a longer daily illumination, plants in northern regions are content with a smaller absolute intensity of light. There is a further possible complication: plants growing in cold regions may require a greater total radiation, because they have to avail themselves of the heat rays in that radiation in order to make their habitat supportable. The same hypothesis would account for the fact reported by Wiesner, namely, that *Hordeum jubatum* growing 540 feet above sea-level has a relative light "minimum" of 1/9 daylight, while at an altitude of 7,500 feet its relative light "minimum" is 1/5.

These examples are enough to emphasize the importance of separating, in analysis, the light rays of the sun from the heat rays. It may be revealed, upon closer examination, that many so-called heliophytes are really "thermophytes": heat-demanding plants, rather than light-demanding plants. It might well be the case that one and the same species could behave as a shade plant in southern regions, or in the low-lands, and be a sun plant in the north, or in mountains. In the former case the heat radiations would be supra-optimal, in the latter they would be in the optimal region.

In recent years investigations have been carried out upon the influence of the daily period of illumination on plant growth. The pioneers in this field were Garner and Allard (1920–23, –25), who subjected plants to varying "lengths

of day" from 5 to 12 hours, in the latitude of Washington. They found that "length of day" determined to a great extent the time of sexual reproduction, which only occurred if the daily exposure to light were between a certain maximum and minimum time. Below the minimum the plant was sterile; above the maximum giant growth sets in. When the "length of day" was reduced in stages from 12 hours to 5 hours, flower formation occurred earlier and earlier, until for every species investigated, a characteristic light minimum was reached. When, for instance, the late flowering soy bean, "biloxi" form, is subjected to a 12-hour daily period of illumination, the time from germination to flowering amounted to 110 days. When the daily period was only 5 hours, the time amounted to no more than 27 days. In the case of *Aster linariifolius*, with a daily illumination of 12 hours, the vegetative period was 122 days, whereas it was only 36 days with a 5-hour period of illumination. These plants are "adapted" to a short day. On the other hand, there are other plants which require a long daily period of illumination for flowering; an example is given by *Micania scandens*, which will not flower at all with a daily illumination of less than 12 hours.

Experiments in which the normal daily period of illumination has been supplemented by the use of electric light have demonstrated that there is an upper limit of daily illumination, above which normal development does not reach completion. Flowering, according to Harvey (1922; 1924), occurs only above a certain limiting intensity of light (*see also* Arthur, 1927). *Chenopodium album*, for instance, can develop normally under a great deal of light; cereals require a moderate amount, while *Cucurbita moschata* and *Tropaeolum minus* are satisfied with very little. According to Tinckner (1924; 1925), clover under a short daily illumination retains its winter form. Maximov, Yoshii, and others, have found that different races of the same species (such as varieties of wheat) show differences in their response to length of day. To this phenomenon Wanser attributes the difference between winter and summer wheats (1922).

The influence of light upon the living plant, then, depends not only upon its quantity and quality, but also upon the distribution in time of the illumination. The mere summation of light during the vegetative period, a procedure which has been advocated by some authors (Warming-Gräbner, 1915–

18), is no adequate expression of the ecological light climate. Alternation of day and night, involving as it does alternation of assimilation and translocation, is of obvious importance for the material economy of the plant. The literature of photoperiodism has been admirably summarized by Kellerman (1926).

The facts discovered by Garner and Allard throw light upon several phenomena which have been observed by plant geographers. Some plants, radishes for example, do not flower when put into a tropical climate. Again, beetroots are known as biennials, but in Alaska, in the Arctic, they behave as annuals. It may be assumed that every species reaches the optimum of its development only within definite latitudes, i.e. under definite light conditions. The failure of many experiments on acclimatization which have been attributed to unsuitable temperature conditions may on closer investigation be shown to be due to unsuitable conditions of illumination.

These discoveries combine with those of Klebs to demonstrate that, for normal development, a certain "constellation" of environmental conditions is necessary. According to Adams (1924), the rate of growth is primarily dependent upon the amount of assimilate formed. Every individual needs a specific amount of assimilate for its full development; provided this amount is available, it matters less how the light is distributed throughout the day. A continuous weak illumination can then replace an intermittent and more intense illumination. Account must also be taken of the formative effect of the light. Below a certain intensity the plant is etiolated, while an excess of light will inhibit flowering. Nightingale (1927) and Lamprecht (1928) have done some work upon the influence of different lengths of day upon the chemical composition of certain plants.

The need for light among the different competitors of a plant society differs widely among the different species. To investigate this relationship quantitatively Wiesner (1907) introduced the conception of the light minimum. He measured the light intensity in the darkest parts of a tree where leaves still occurred and functioned, and he expressed the intensity as a fraction of the intensity of the light falling upon the freely illuminated leaves above, measured at the same time. In Table VI are given some examples of these measurements.

TABLE VI

RELATIVE "LIGHT REQUIREMENT" BY WIESNER'S METHOD

Plant.	Relative Light Minimum.	Observer.
Larix decidua . . .	1/5	Wiesner (1907)
Betula verrucosa . .	1/7–1/9	Wiesner, Hesselmann (1904)
Pinus sylvestris . .	1/9–1/11	,, ,,
Pyrus malus . . .	1/1·6–1/6·8	Stålfelt (1921)
Quercus pedunculata . .	1/26	Wiesner
Picea excelsa . . .	1/28–1/33	Hesselmann
Fagus sylvatica . . .	1/60–1/80	Wiesner
Buxus sempervirens . .	1/100	,,

For every species growing under consistent conditions the relative light minimum seems to have a fairly constant value, a value which decreases with decreasing geographical latitude, or height above sea-level. The light minimum seems to change even with the nutritive conditions of the soil; Hesselmann mentions that hazel bushes have on poor soil a very thin crown with a light minimum of 1/18–1/20, and on better soil a thick crown with a light minimum of 1/50–1/60. Similar observations have been made by Ramann (1893). The cause of this relationship between soil nutrition and the relative light minimum may rest in the fact that well-nourished plants, especially plants provided richly with nitrogen, form more chlorophyll, and are deeper in colour than plants growing on a poor sandy soil. Rich manuring of the soil may compensate to some extent for poor illumination, for the richer the leaf is in chlorophyll the higher is its assimilation per unit area (Lundegårdh, 1924, *a*, p. 81). Variations in chlorophyll content as great as 70 per cent occur.

Every tree, therefore, can grow within certain limits of illumination, and it was possible, using the methods introduced by Wiesner, to gain some quantitative data upon this point. In spite of its great practical importance, however, the matter has received very little attention since Wiesner's paper (Stålfelt, 1924). In America, and its colonies, W. H. Brown (1919) and Lee (1924) have collected data on the influence of illumination upon succession among conifers. In European forests it has been observed, too, that bushes whose

PLATE II

(b) Beech wood with scattered oaks, which have assumed completely the habit of beeches. The crowns of the trees growing close together are broom-shaped.

(a) Oak tree. The angle of branching is very wide, and the crown is able to intercept a correspondingly greater amount of light.

light requirements are low gain easy entrance into thin oak woods. Formerly the Danish islands were covered with oak woods. Subsequently beeches migrated into these woods and in many places have spread throughout the areas formerly occupied by oaks (Plate II b). Pure oak forest, in fact, is quite rare (Vaupell, 1863). (*See also* Adamson, 1918.)

Light is only one of the factors in this succession of the tree flora. Changes in the constitution of the soil, brought about by the changing flora itself, hasten the transformation of the habitat. The soil of a fir forest, for instance, is totally unsuitable for deciduous trees. When fir trees are established on the site of a destroyed oak wood, it is found that although individual oaks may still come up, they will never again of their own accord form a closed formation.

It is not yet known whether or not the light minimum is related to the light curve of assimilation; it would certainly be erroneous to imagine that leaves below the "light minimum" are also below the compensation point. According to Hesselmann (1904), the innermost leaves of a hazel bush are able to form starch. Stålfelt found, too (1924), that in fir trees the most shaded needles received enough light to assimilate carbon dioxide. The cause of the dying off of the innermost parts of trees is not so much poor assimilation as more probably a lack of water and salts. Stålfelt has mentioned that the needles of fir trees remain longer on the tree on the northern side than on the southern side, a result which would not be expected if assimilation were the deciding factor. In the competition for available water and salts, young needles and the vigorously assimilating apical leaves of deciduous trees are at an advantage, and the leaves within the crown of the tree are more poorly served.

The juvenile forms of trees have been very little investigated, and it is possible that the question of light minima may play a part here. A young tree, shooting up under the canopy of an older one, needs less light than the adult. Physiologically it behaves exactly like a species with a low light minimum; but it has yet to be discovered whether this behaviour is correlated with its different habitat.

The range of anatomical and physiological adaptation of leaves plays an important part in the rejuvenation of forests and in succession in natural habitats (Fig. 14). Certain trees, the birch and the ash for instance, are unable to produce any typical shade leaves; their inner leaves can hardly

be distinguished from the outer leaves. This limited plasticity is certainly an important reason for their high light demands (Hesselmann, 1904).

A further question of importance in ecology is the absolute utilization of the available illumination. Consider a birch, a fir and a beech under the same light intensity: they will naturally produce different amounts of carbohydrate per day. In estimating the net assimilation yield (assimilation minus 24 hours' respiration), not only is it necessary to know the assimilation per unit leaf area, and the respiration
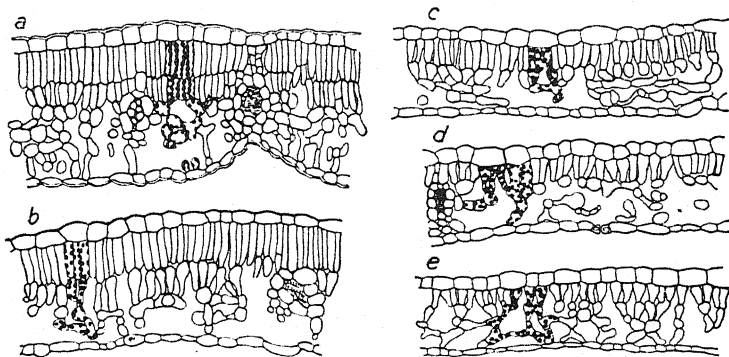
Fig. 14.—Transverse sections of leaves of *Corylus avellana*: (a) from the southern side of a bush, (b) from the northern side (both in the sunlight), (c–e) shade leaves, (c) light = 1/20, (d) light = 1/33, (e) light = 1/50. (After Hesselmann, 1904.)

per unit weight, but also the full extent and arrangement of the total leaf surface of the tree. Thus it is evident that a low efficiency of assimilation can be compensated by a large and suitably disposed leaf surface. In firs, according to Stålfelt (1921), this state of affairs is realized. Fir needles contain only 10·6 mg. chlorophyll per 10 gm. dry weight, compared with 15 mg. in pines (*see* Table V). To compensate for this, however, the fir has a considerably greater total leaf surface, and an excellent leaf arrangement for absorbing the predominantly oblique light of northern latitudes. Compared with most deciduous trees, conifers display a very low efficiency in their assimilation; but in spite of this their quantity of wood production exceeds that of many deciduous trees, such as the beech. These examples suffice to show how complex the adaptation to the light factor can be in nature.

Trees form the topmost layer in the compound society which we call forest. In a typical closed wood, where the

tree canopy forms a continuous layer, the intensity of the light which penetrates beneath depends upon the "light minimum" of the dominant tree species (Fig. 15). On this account the sub-vegetation of an oak wood has quite a different aspect from that of a beech wood. In these two types of wood, the soil conditions can be about the same; the decisive factor, therefore, is the light. But in other instances, alder woods, and fir woods, for example, the soil deviates in character so markedly from the normal that it is difficult to disentangle any influence due to the light alone.

A forest may be divided into several vertical layers; the
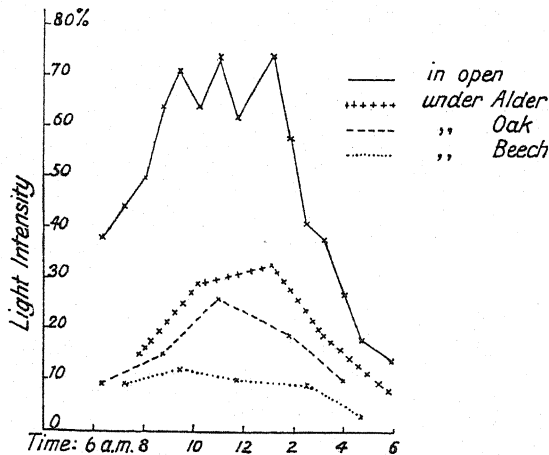
FIG. 15.—Simultaneous light curves made in a wood and in the open, on May 23.
(After Vallin, 1925.)

following strata can generally be distinguished: 1, tree layer; 2, bushes; 3, tall herbaceous plants, such as ferns; 4, prostrate herbaceous plants (the real "ground vegetation"); 5, liverworts and mosses; and 6, algæ. The forest flora can be divided into two groups: facultative and obligate shade plants. The first group includes plants which can occur as phenotypic sun forms, and which are therefore at the lower limit of their light requirements in a wood. To this group belong especially the layer of bushes and tall herbaceous plants (Fig. 16), for example, *Corylus avellana*, *Rosa canina*, species of *Rubus* and *Ribes*, *Sambucus nigra*, *Lonicera periclymenum*, *Pyrus malus*, *Crataegus*, *Prunus spinosa*, species of *Salix*, and so on. Bushes are also encountered outside woods. In thick woods, such as beech, they disappear altogether.

In the third region, the upper herbaceous layer, a great number of plants are found, which occur also in meadows, and even on the sea-shore: *Solanum dulcimara*, for instance, which can occur either as a large-leaved form, or as a hairy sea-shore form, similarly *Lythrum salicaria*, *Spiraea ulmaria*, *Geum rivale*, *Melandrium rubrum*, etc. In addition there are numerous shade-loving forms, whose near relatives are heliophytes: the species of *Poa*, for example.

Then there is a number of genuine facultative shade plants. Only by culture experiments of genetically pure forms, first in the shade, and then in the open, can it be decided how far-reaching is their capacity for adaptation; and until such work is carried out, no definite statement as to their behaviour can be made (Turesson, 1922; Vallin, 1925).

In the flora of a deciduous wood can be found certain plants which are indubitably heliophytes. These: *Anemone nemorosa*, *Corydalis*, etc., flower in the spring before the leaves appear on the trees, and so are able to benefit by the full light of spring. In this short time they store up a capital of carbohydrates, which serves them for the whole vegetative period. All these spring-

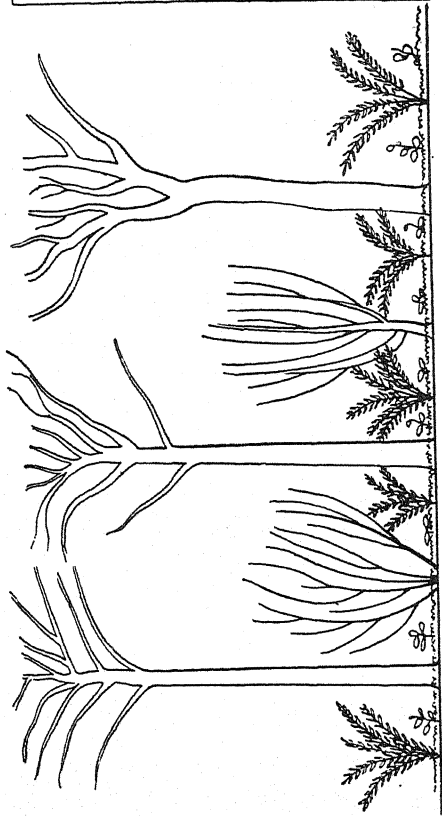| Heliophytes	Hemi-Sciophytes	Facultative Shade. Pl.	Obligate Sh. Pl.	"
1. Trees	2. Bushes	3. Taller Herbs	4. Small Herbs	5. Mosses & Algae

FIG. 16.—A diagrammatic representation of the stratification of plants in a wood.

flowering plants possess subterranean organs, and during the
summer they are more or less in a resting state.

Several observations have been made upon the change
of light climate in a deciduous wood during the spring
(Diels, 1918; Salisbury, 1916; Markgraf, 1922). The
period before the leaves unfold their leaves is called by
Salisbury the light phase, and the period when the foliage
is open, the shade phase (1916). During the first period the
intensity of light in a British oak wood is from 30 to 100
per cent of the maximum intensity in the open; during the
second period the percentage is no more than 0·16 to 1·3.
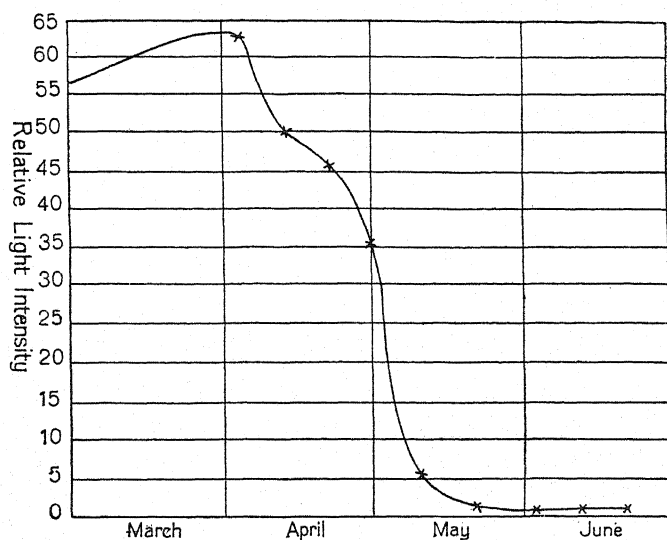
FIG. 17.—The decrease in the light factor in a *Quercus robur-Carpinus* wood during
the unfolding of leaves.   (After Salisbury, 1916.)

The actimometer was employed in this work; changes in the
quality of the light, therefore, would not be registered.
Using the "Graukeilphotometer," Markgraf determined the
midday light intensity in Bredower forest to be 7·1 units
in April, and 4·37 units in June (1922).

Figures 17 and 18, taken from Salisbury's paper, give
some idea of the relation between illumination and vegetation
in an oak wood.   As early as January newly expanded leaves
are found upon *Ficaria verna*, *Mercurialis perennis*, and
Primula acaulis, and these plants are found in the deepest
shade of the woods. *Scilla nutans* and *Arum maculatum*
appear in the middle of February, and *Anemome* and

E

Galeobdolon luteum only in March. These plants occupy the parts of the wood which are better illuminated. On the average, according to Salisbury, forest plants flower a month earlier than plants growing in the open. Possibly they are "adapted" to the shorter length of day.

In addition to these spring plants, whose leaves are formed for the most part like sun leaves, the forest flora contains a number of obligate shade plants, whose development continues for the whole vegetative period, and whose leaves are typically sciopyllous. Many of these plants put forward their leaves in the spring and remain actively growing until the
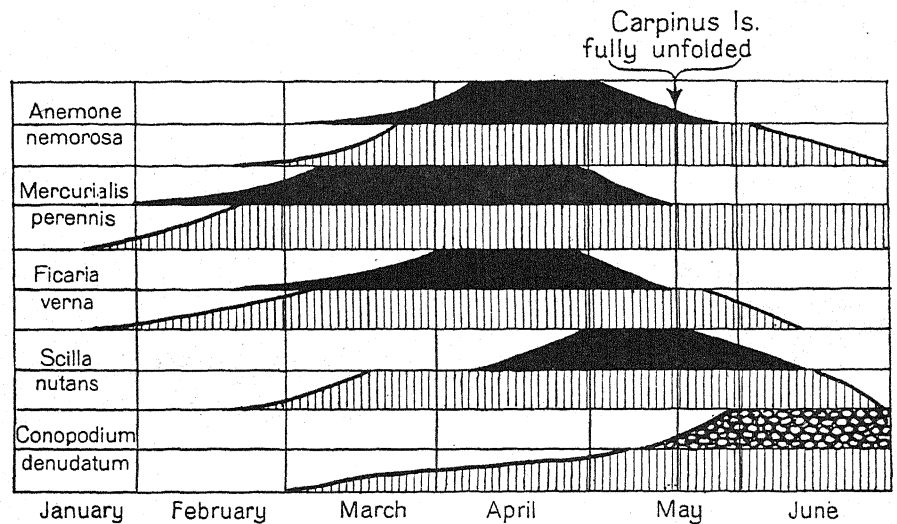
FIG. 18.—Period of functioning of leaves (shaded), and formation of flowers (blackened) in an English deciduous forest. (After Salisbury, 1916.)

autumn; and in the autumn they probably have a second period of vigorous assimilation. Among these plants, which form the permanent ground vegetation, may be mentioned *Oxalis acetosella*, *Galeobdolon luteum*, *Stellaria holostea*, *Geum urbanum*, *Veronica chamedrys*, *Viola sylvestris*, and many others. Some of these plants remain active even throughout the winter. Other shade plants such as *Athyrium* and *Dryopteris* do not begin their development until May or June, at a time when the trees are already in foliage. To this group belong also *Holcus lanatus*, *Deschampsia caespitosa*, and other forest grasses, and also species of *Rubus* and *Rosa*. Plate III shows two aspects of the ground vegetation in a mixed deciduous forest.

PLATE III

Spring and summer aspects of the ground vegetation in a mixed deciduous forest. Above, *Anemone nemorosa*, etc.; below, *Melandrium rubrum, Stellaria holostes*, etc.

The obligate shade plants of a wood either cannot endure full sunlight at all, or can merely eke out a miserable existence in it. The physiological difference between sun and shade plants has already been discussed; and what was mentioned there for the higher plants holds true for sciophytes among the lower plants, the mosses, liverworts, and algæ. In the economy of these plants, it is not only the shape of the light-assimilation curve which acts as a determining factor, but also the water
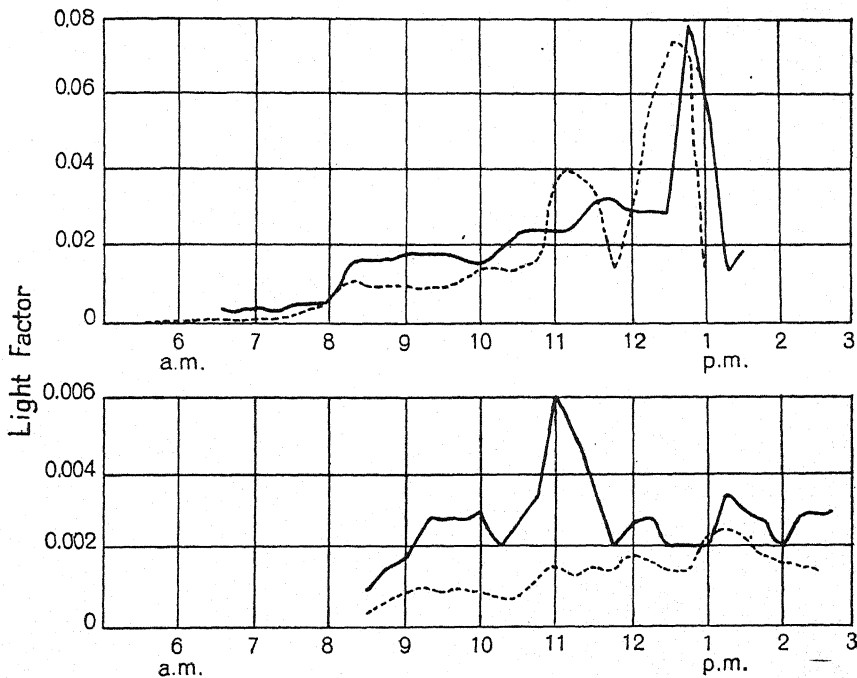
FIG. 19.—The light factor of two habitats of *Oxalis acetosella*, measured on September 6, by the method described on page 11. The upper curve is from a habitat in a wood, the lower from a habitat shaded by ferns. The continuous curves represent the blue and violet radiation, and the dotted curves red and green radiations. (Lundegårdh.)

supply. This latter is obviously of great importance in those lower plants which lack the capacity to cut down their transpiration.

Of the assimilation of algæ and mosses, and of their light requirements very little is known. Scarcely any work has been done under natural conditions, and it is unsound to draw conclusions from laboratory experiments. To all appearances algæ and mosses are often satisfied with extraordinarily small light intensities. One might conjecture that their assimilation

is relatively more vigorous than that of phanerogams, and that their respiration is relatively less so. It has been observed that the chloroplasts of algæ occupy a greater proportion of the cell than those in higher plants; moreover, in these lower plants all superfluous material expense, such as mechanical tissue, is dispensed with. It is, therefore, not surprising,
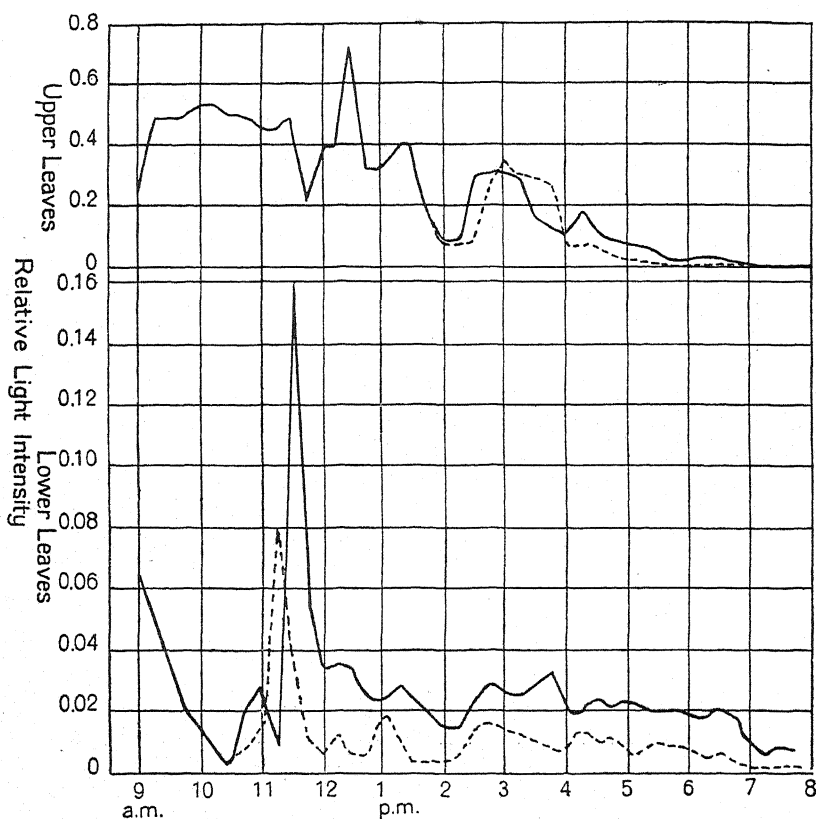

FIG. 20.—The light factor in the region of the lower and the upper leaves of a potato field. Curves taken simultaneously on August 9. (Lundegårdh, 1923, d.)

perhaps, that these plants can flourish in situations where the only light available is that "left over" by higher plants.

For the measurement of light intensities in forests the photometer described on page 11 had been employed (Lundegårdh, 1923, d). In this apparatus both the red rays and the violet rays are recorded; in a wood the red-yellow rays are transmitted more than the violet. In the open, on a clear day, the quotient red-yellow/blue-violet was approximately

0·7. In the wood the ratio was increased to 2·0 or 3·0. The diurnal course of such light curves is illustrated in Figures 19 and 20. Extreme shade plants, such as *Oxalis acetosella*, which grow at the level of the mosses, seldom intercept light intensities greater than 1/100 that of the light intensity in the open, and often they have to be content with 1/1,000 of the illumination in the open.

Continuous records of light intensity taken in a wood present a much more irregular curve than that of similar records taken in the open. The reason for this is not far to seek, and is of some ecological significance. As the sun moves across the sky during the day, flecks of sunlight pass over the ground, giving successive patches of ground vegetation temporary bursts of photosynthetic activity; these flecks are recorded as maxima on the diurnal curve of illumination.

When the light-assimilation curve and the respiration intensity of a shade plant is known, its daily carbohydrate balance can be calculated (Lundegårdh, 1921, 1922, *a*). The leaves scarcely ever exhibit excessive assimilation, so that the respiration remains constant, and in a shade plant the errors due to stomatal movement are smaller. Such calculations for *Oxalis acetosella* often lead to the conclusion that the plant is living under its minimum; that its expenditure in respiration is exceeding its income in photosynthesis. Despite this the leaves remain green, and function normally. The positive periods of assimilation of *Oxalis* are spring and autumn. Except for outbreaks of assimilation in the flecks of sunlight, the leaves are below the compensation point during the summer.

The respiration of shade plants is, as a rule, less than that of sun plants (Lundegårdh, 1921, 1924, *a*, p. 89). Even sun and shade leaves of the same species can be distinguished as regards their intensity of respiration. It follows, then, that the compensation point in shade plants occurs at a much lower light intensity than that in sun plants. In a number of sun leaves observed by various authors (*see* Lundegårdh, 1924, *a*, p. 89) the light value at the compensation point (for 18°–20° C. and 0·03 volume per cent carbon dioxide) was found to be between 1/75 and 1/13. The highest values were given by *Pinus sylvestris* (1/25) and *Picea excelsa* (1/13). When these trees are growing in deep forest shade their respiration must exceed the assimilation. At the compensation point of a number of shade plants, light values of 1/300–1/100 were

found; even in the darkest shade, then, these plants will assimilate with some profit.   Geiger (1927), using *Aspidistra*, found a compensation point as low as 275 lux (i.e. 1/330).   This seems to support the observation made by Kastner (1911), namely, that *Urtica dioica* and other plants are able to grow in habitats with light values as low as 1/150–1/175 full daylight.

In order to gain some idea of the whole carbohydrate balance, the respiration in the dark must also be taken into account; it will then be seen that the "hunger limit" does not lie immediately above the compensation point.   Moreover, with a higher concentration of carbon dioxide, the light value at the compensation point is reduced.

R. McLean (1919) has published some observations upon the conditions of illumination in a tropical rain forest.   As Schimper has so vividly described, the trees in a rain forest do not form a continuous flat canopy, as do the trees in a mid-European forest.   On the contrary, the height of the trees is very variable, bestowing on the forest an irregular contour when viewed from a distance.   In the forest investigated by McLean in South Brazil, the dominant trees were *Mimosaceae*, whose delicate leaves let through a great deal of light.   The bush layer, on account of the beautiful mosaic of the leaves, casts the deepest shade.   According to McLean, the moving flecks of sunlight play an important part in the illumination of the ground flora; for the normal light intensity upon the ground was 1/140, while the flecks of sunlight reached intensities of 1/8 of those in open sunlight.

In a tropical rain forest there is no regular period of leaf fall as there is in a deciduous temperate forest.   Thin and thick-leaved species are mixed, and the latter carry their leaves for more than one year.   F. Shreve (1914) has shown that in the rain forest of the Jamaica mountains sclerophyllous trees occupy the top layer, and mesophyllous plants the lower layers; this regional differentiation may depend upon the differences in humidity.

There exists an extensive literature upon the periodicity of leaf formation and leaf fall, into which we cannot enter here (Jost, 1923).   Suffice it to be said that the periodicity can be profoundly affected by external conditions.   Northern trees, like *Quercus robur*, which have been planted in the tropics, retain their leaves the whole winter.   Internal factors, too, undoubtedly play some part in the phenomena of leaf fall and leaf renewal; for among tropical trees there is a great lack of

agreement between the age of the leaves and the time of leaf fall. The resultant behaviour of a leaf seems to be dependent upon so many internal and external factors that it is difficult to decide whether its functioning is regulated primarily from within or without. The critical experiments which alone would throw light upon the matter, have not yet been carried out.

From the ecological point of view the fact of greatest importance is that under the constant conditions of illumination of the tropics, photosynthesis can be continued throughout the year. All botanists in the tropics have observed that the plants carry relatively few leaves. The efficiency of the leaves is much greater, and the need does not exist for a type of leaf which will embrace a wide range of light conditions, such as our northern trees require.

In a tropical rain forest, not only are there more biological types, but their development is more extreme than that of the biological types in temperate and sub-Arctic regions. This is probably owing to the favourable conditions of humidity, light, and temperature. The shade plants go to much further extremes than the temperate shade plants in their economy of structural material. In the most deeply shaded regions of the Jamaica forest Shreve has found plants such as *Peperomia pelucida*, which have only a single layer of mesophyll, and the filmy ferns, whose leaves are only one cell thick.

In a typical rain forest there is no area which is not covered with green plants; the tree-trunks are laden with epiphytic algæ, mosses, ferns, and flowering plants; even the leaves carry epiphytes upon them. This amazing vitality, variety, and denseness of vegetation is only possible because all the factors are favourable to growth.

Even in the tropics there are all transitions from the richness of the rain forest to the poverty of the forest in which some factor is from time to time limiting. The teak forests of Java, for instance, occur in a region where a dry period alternates with a rainy season, and the vegetation, which in this instance is limited by water, is characterized by relatively fewer species (Karsten and Schenck, 1905).

The regional vertical distribution of vegetation reaches its highest development in the forest. But almost everywhere such a distribution can be found more or less completely developed. An exclusively "two dimensional" arrange-

ment of vegetation only occurs under two conditions: when one individual species spreads so quickly that the individuals leave no soil space (as with certain grasses, and *Polytrichum* and *Sphagnum*), and upon very poor soil, such as rocks and sand dunes, where, since other factors are limiting, competition for light does not come into question. The first condition is a transitional one, and it seldom becomes stable unless the second also plays a part. As soon as the habitat becomes tolerable, the pure association is destroyed, and straightway the struggle for light begins. Even in open ground there is a definite regional distribution of species into "taller" and "shorter," where the latter receive less light than the former. The most conspicuous in the struggle are naturally those with large shading leaves (as, for instance, the plantain on a lawn). In a thickly populated meadow it is difficult to decide sometimes whether the light factor or the soil factor decide the issue. For every square centimetre of ground is occupied, and the vitality of the root system, its mode of branching, its depth, and so on, play a very important though obscure rôle in the initial struggle for space. This struggle leads to a regional distribution of the subterranean parts, a distribution perhaps more decisive ecologically than the subærial distribution of assimilatory organs (Woodhead, 1906; Sherff, 1913; Hanson, 1929).

Light in meadows and similar "shallow" formations is generally a factor in the maximal region, and it therefore plays a secondary part in the distribution of vegetation. Even in these shallow formations, however, there are little shade species, which are protected by the taller vegetation above, and a determination of the distribution of light in such a habitat would be of great interest. An idea of the shading present in a potato field is given by the curves in Figure 20. The light falling upon the topmost leaves reaches an intensity of 0·4; the intensity reaches only 0·03 underneath. Flecks of sunlight are probably as important here as they are in woods.

In floristic plant geography it is customary to determine the degree of frequency in which the plants occur statistically; and unfortunately the "denseness" of the vegetation and its regional distribution has received very little attention.

By "denseness" of vegetation is understood the area which any individual covers or shades. This concept is not to be confused with that of the "minimal area," introduced by Nordhagen (1923), which latter is an expression of the

average distance of the individuals from one another, irrespective of what size they are.

To determine the "denseness" of the vegetation a sample area of one square metre in size is pegged out. On this area there grow equally well, let us say, *Oxalis acetosella* and *Melandrium rubrum*, so that, if a quadrat measuring one square decimetre is laid out ten times, *Oxalis* and *Melandrium* occur each time. These two would both be given a *frequency* of 100 per cent. But the *Oxalis* plants are very thick, covering almost every square centimetre of the ground, while the plants of *Melandrium* stand markedly apart from one another.
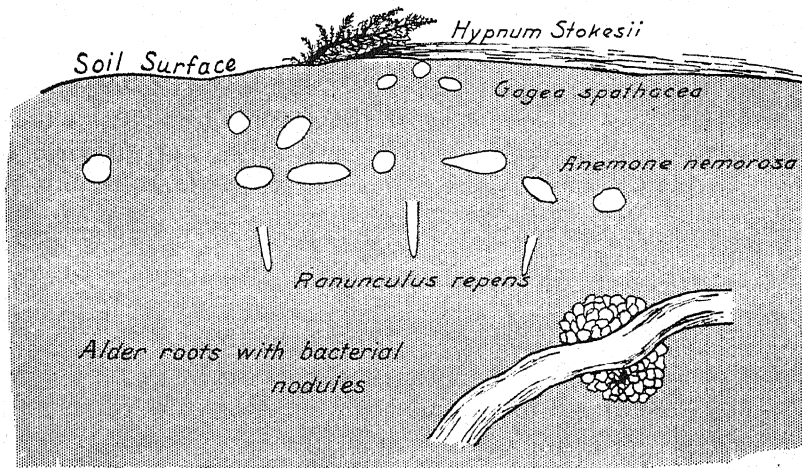
Fig. 21.—Diagram of the soil strata of an alder wood, to illustrate the "complementary associations" (Woodhead)) of the subterranean organs. (Vallin, 1925.)

The minimal area of the latter is therefore considerably bigger than that of the *Oxalis*; on the other hand, the *Melandrium* plants have a higher "denseness" than the *Oxalis*.

Suppose there is growing on the sample area a specimen of *Rubus idaeus*. In spite of its low frequency of 10 per cent, this plant possesses a high degree of "denseness." In addition, its leaves are some distance above the ground, and their shading effect upon the plants below is therefore much increased. In assessing the influence of this plant upon its competitors its degree of "denseness" must be taken into account, its "vertical distribution," and the arrangement of its roots.

It will be obvious from these considerations that the

observation of morphological characters alone will not give a reliable estimate of the influence of a plant upon its competitors. The degree of "denseness," as such, is extremely difficult to measure. It is easier to assess the plant's influence indirectly by measuring the physiological environment around it: the illumination conditions above and below the plant.

In the foregoing discussions we have been concerned with habitats exposed to full light, and where the distribution of the light was determined by the plants alone. There are also habitats, such as caves and rock crevices, from which a great proportion of the daylight is cut off, and here are to be found the most extreme shade plants that are known. These plants are able to live in the very poor light at their disposal, partly owing to the luxury of the water supply, and to other favourable environmental conditions.

In their anatomical structure the shade plants exhibit the greatest economy of material. It is therefore not surprising that the very simply organized mosses and algæ can benefit from the most unfavourable conditions of illumination. The most frugal in their economy are the green and especially the blue-green algæ; in these plants the chlorophyll fills the whole cell, and the surrounding structure is of the simplest conceivable nature.

The moss *Schizostega*, which is extraordinarily well adapted to poor light, has been found by the author in caves where under the best conditions the light intensity did not exceed 1/600. In the eastern Alps, according to Lämmermayr (1911, 1915), the *Schizophyceae* penetrate further than any other plants into the caves; they have been observed, for example, in the Drachenhöhle at Mixnitz, 60 metres from the entrance at a relative illumination of about 1/1,800. Morton and Gams (1921) have found algæ growing at a relative illumination of 1/2,500. In the caves at Macocha the author has found algæ, mosses, and even certain ferns, growing in the neighbourhood of an incandescent lamp, which is only lit for visitors. A definite zonation was to be seen here, around the source of light: ferns nearest, then mosses, then algæ.

In view of the extraordinary frugality of *Cyanophyceae* and certain *Chlorophyceae* toward light, it is not surprising that they are also encountered in the ground and in rocks. Algæ form an integral part of the soil life, occurring at depths of from 25 to 60 centimetres (Esmarch, 1914; Robbins, 1912;

Peterson, 1915; Bristol, 1920; Russell, 1923). Probably the algæ at the greatest depths have been carried down by worms or by the plough; and it is known (Roach, 1928) that they are capable of a heterotrophic metabolism.

On wet sand by the sea, and on damp sandy moors, there occurs, a few millimetres under the surface, a layer of *Cyanophyceae*. The mucilaginous envelope which surrounds the algæ binds the sand particles together into a thin crust (Warming, 1915–18). These algæ are probably autotrophic, although the light intensity they receive is as weak as that of the deepest forest shade, and though the algæ always occur *under* the surface.

Even in rocks, when they are sufficiently transparent, and when microscopic clefts are present, algæ have been found to occur. Diels (1914), who has described such an endolithic flora in the Dolomites, has found *Trentepohlia aurea* and species of *Gleocapsa* in a thin layer from four to eight millimetres under the surface of the rock (Fig. 22). Examination of the penetration of light through the stone showed that the penetration of the red and yellow rays was relatively
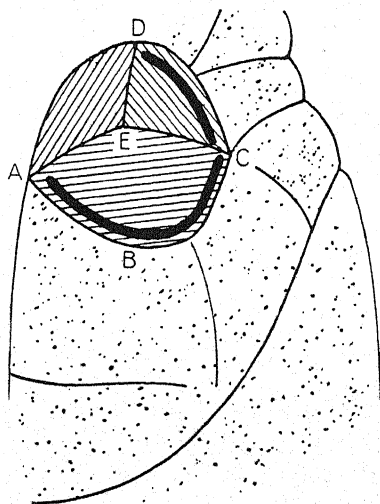

FIG. 22.—A piece of dolomite rock, fractured with a hammer, showing the position of endolithic algæ (shaded). (Diels.)

greater than that of the shorter waves. Two millimetres below the surface, these rays are reduced to between 0·8 to 2·0 per cent; and at a depth of four millimetres, to 0·01–0·03 per cent. Since the algæ occur at depths of from six to eight millimetres, extremely small quantities of light, of the order of 1/10,000, must suffice for their metabolism; and the compensation point of these organisms must lie far below that of Phanerogams or ferns. Harder (1923, *a*) determined the compensation point for the moss *Fontanalis*, and found that it lay between 1/300 and 1/500 full sunlight, i.e. between 95 and 152 metre candles. It is of interest that the position of the compensation point depends upon the intensity of the light in which the plant has been growing. Cultivating the plant

in weak light lowers its compensation point. Harder (1923, *b*) has discovered a similar adaptation in certain *Cyanophyceae*.

In water, especially in the sea, there is to be found a striking vertical distribution of plant life. The intensity of light in water decreases with the depth; according to Schmidt (1908), the relative light intensity is 0·549 at a depth of one decimetre, 0·358 at a depth of one metre, and 0·014 at a depth of 100 metres. When the water is disturbed the decrease in light intensity with depth is enormously increased. In the Baltic in August, Oberdörfer (1928) found at a depth of fifty metres a decrease in the illumination to 0·000,006. It has long been supposed that this is the determining factor in the zonation of plant life in water. Very little is known, however, about the relation between photosynthesis and illumination among marine algæ.

Kniep (1914) has carried out some work upon the assimilation of marine algæ. The intensity of photosynthesis is somewhat small, varying in *Ulva lactuca*, *Padina pavonia*, *Porphyria laciniata*, and *Asperoccus compressus*, in bright sunlight, between 1·3 and 2·75 mg. per hour per 100 square centimetres. Under the same conditions flowering plants will assimilate from 7·0 to 20·0 milligrams. The most vigorous assimilation recorded by Kniep was in *Fucus serratus*, where the assimilation reached 4·5 mg. per 100 square cm. per hour,—about the same intensity of assimilation as that of a typical shade plant.

The vertical distribution of the *Chlorophyceae*, *Phaeophyceae*, and *Rhodophyceae* in the sea will depend upon their respective assimilation curves; observation upon this problem has been insufficient up to the present (*see* Moore, 1923). *A priori*, one would be inclined to consider the *Chlorophyceae* the sun plants, and the *Rhodophyceae* the shade plants; the former predominate in shallow parts of the sea, and the latter at greater depths, though within each group there are wide variations. (Table VII.)

TABLE VII
THE VERTICAL DISTRIBUTION OF ALGÆ IN THE DANZIG BAY

Depth.	Red.	Brown.	Green.	Blue-green.
0–2 m.	4	11	30	15
2–4	14	14	16	5
4–8	18	15	10	2
8–12	11	9	3	—
12–18	9	6	2	—
18–25	7	5	—	—

(From Lakowitz. (*See* Sernander, 1917; also Geitler, who published some observations on distribution in fresh water (1922); and Pascher (1923).)

As would be expected, the intensity of assimilation decreases with the depth. This has been confirmed by Jönsson, who lowered a moss, *Climacium dendroides*, in a closed vessel to different depths, and measured the resulting assimilation (Fig. 23).

The constitution of the light changes with the depth below sea-level. Red and infra-red radiations are absorbed to a much greater degree than the blue or violet rays. According to Ewald and Grein, the intensity of red light is reduced to 3 or 4 per cent at a depth of only five metres, and at 100
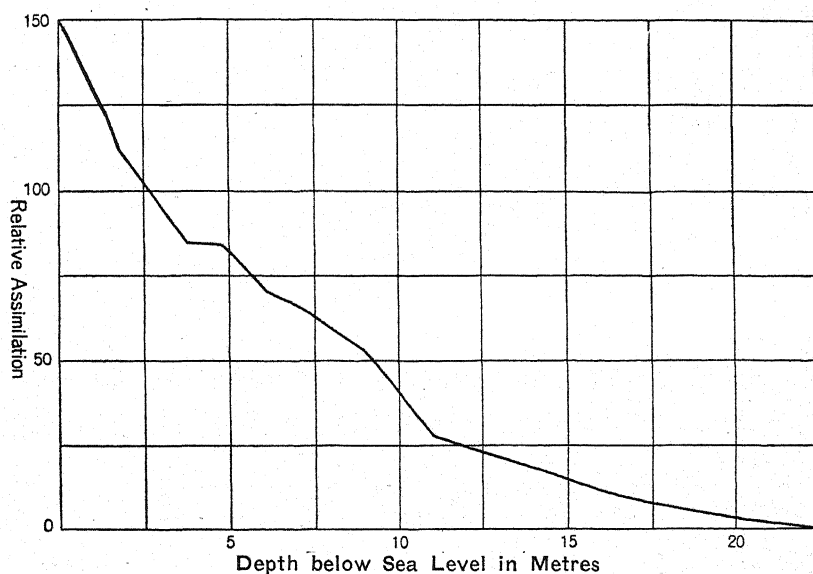
Fig. 23.—The decrease in the assimilation of *Climacium* with increase in depth below the sea. (After Jönsson.)

metres it can scarcely be demonstrated, while the blue and violet rays penetrate to a depth of 1,500 metres. Oberdörfer (1928) reports a decrease at a depth of ten metres to 2·5 per cent in the red, 5·1 per cent in the blue and 12·4 per cent in the violet rays.

In the light of these facts, the colours of algæ have been considered by Englemann (1883–4), who was the first to observe that algæ assimilate in light complementary to their own colour. Recently Wurmser (1921) has carried out research with red and green algæ in light of different wave lengths; according to this, red algæ in green light assimilate more vigorously than green algæ under the same conditions.

In a very exhaustive investigation Harder (1923, *b*) found that *Phormidium foveolarum* has a maximum assimilation in the longer or shorter wave lengths of the spectrum, according to the colour of the plant itself. In red light the blue races assimilate most efficiently, and vice versa. In this respect the "chromatic adaptation" described by Gaidukow (1904) is interesting; material genotypically pure is coloured red in blue light, and blue in red light. (Boresch, 1921, 1922; Harder, 1923, *b*.)

Thus the colouring matters phycoerythrin and phycocyanin which occur in addition to chlorophyll in algæ, quite possibly take part in the process of assimilation; upon this rests the probability of Englemann's theory of regional distribution of marine algæ. Green algæ in the blue-green twilight of the deep sea would scarcely assimilate at all, while the brown and red algæ are enabled to utilize the light better on account of their complementary colouring. Oltmanns (1905), on the other hand, does not consider that the colouring matters play such an important part, and that the *Rhodophyceae* are shade plants and the *Chlorophyceae* sun plants. It is undoubtedly the case, as Boresch (1922) and Harder (1923, *b*) have recently shown, that the efficiency of assimilation can vary within wide limits according to the previous history of the individual, even in the same species. It seems that both hypotheses have to be taken into account in the consideration of the regional distribution of a marine flora; such a distribution, then, might be determined by the following two considerations:

An alga can live at greater depths, the more closely its assimilation curve approaches the shade type, and the lower its compensation point lies. In the limiting case a green "shade alga" could live at greater depths than a red "sun alga." Secondly, an alga can live at greater depths, the more its own colour is complementary to that of the light falling upon it. Other things being equal, then, a red alga is more efficient than a green alga, at some distance below the surface of the water. Which of these two types of adaptation determines the distribution of algæ in any particular instance must be a matter for further study.

In conclusion some mention must be made of the distribution of light in some English lakes, upon which Pearsall (1920) has carried out some observations. Figure 24 represents the decrease of light intensity with depth, the short

wave lengths only being measured here. It will be seen that at a depth of one metre the intensity of light is reduced by 60 to 90 per cent. To compare the reduction of light intensity with the zonation of the plants, Pearsall used rather a rough method, based on the principle that a white disc of seven cm. diameter is invisible when the light intensity drops to 2 per cent of its original value; and he found that this light intensity marked the lower level of vegetation in
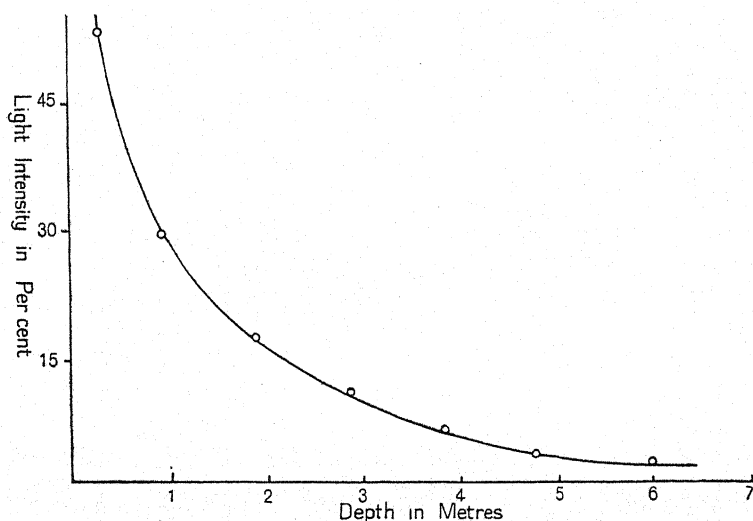

FIG. 24.

six out of the ten lakes he investigated, the depth naturally varying with the degree of transparency of the water. In the zonation of other plants, as *Littorella*, *Isoetes*, and *Nitella*, other factors, especially the soil conditions, seem to play the major part.

In the sea, too, in the upper relatively bright zones, other factors, such as currents, surf, and the ebb and flow of the tides, play a more important part than light in the distribution of the vegetation.

APPENDIX

Illumination of 1 Heffner candle=0·9 illumination of 1 standard candle. The Heffner candle is used in Germany.

1 lux=0·093 foot candles.

1 Bunsen unit:—the standard proposed by Bunsen and Roscoe for the colour change of light sensitive paper. It is the reciprocal of the time taken in seconds for the light to darken the paper to the standard tint (Wiesner, 1907).

CHAPTER III

THE TEMPERATURE FACTOR

TEMPERATURE is the "master factor" in the distribution of vegetation over the earth, though its action is always interwoven with those of light and water. The most local differences in the temperature conditions can engender marked differences in the zonation of the flora and in its distribution, though these differences do not reach those extremes occasioned by local variations in the light climate.

The source of heat for the surface of the earth is the sun. As has been already mentioned, fully 80 per cent of the total solar radiation consists of infra-red rays. This does not, however, presuppose a close parallelism between the light climate and the temperature climate. Indeed, such a parallelism often does not exist at all.

The light climate, as a general rule, follows the latitude, although the degree of clouding modifies this relationship over wide areas. The temperature climate, by which can be understood the air temperature six feet or so above the ground, depends largely upon the soil temperature; which in its turn depends, not upon the amount of radiant energy alone, but also upon absorption, the specific heat, the nocturnal radiation, and other physical phenomena depending upon the structure and water content of the soil (Hann, 1915). Ocean currents, too, play a very important part in the determination of the temperature climate. The British Isles, for instance, enjoy a far more favourable climate than other regions at the same latitude, owing to the influence of the Gulf Stream.

On account of the heat reserves accumulated in the earth during the summer, and given up again during the winter, the contrasts in high latitudes, which would otherwise be very sharp, are markedly moderated. This applies especially to the coastline, where the sea acts as a great thermostat.

The temperature change between night and day, summer

and winter, is therefore far less abrupt than the change in illumination. An accumulation of light energy similar to the earth's accumulation of heat does, however, take place, only the storehouse is the plant itself, whose surplus carbohydrate, manufactured in the day or through the summer, tides the plant over the night or the feeble illumination of the winter; and the light is accumulated as chemical energy.

The heat accumulated by the earth is very seldom sufficient to compensate adequately for the cold of winter, or even for the cooling during the night, and in the plant itself may be found certain characteristics which enable it, indirectly, at any rate, to withstand cold. Thus the radiating surface is reduced, by leaf fall in winter, and by the sleep movements of certain leaves in summer (Jost, 1923); by protection against transpiration, by high osmotic pressure, and by the location of winter storage organs beneath the soil.

It is impossible here to discuss in detail the enormous variety of morphological and physiological adaptations against temperature extremes. The more characteristic of them will be passed in review in the following discussion.

Beside the temperature extremes which exclude from a habitat those species whose range of adaptation is too narrow, the annual and diurnal course of temperature has a profound significance for the metabolism of the plant. It is, first of all then, necessary to discuss the relationship between temperature and the fundamental processes of the plant, growth, assimilation, and respiration.

1. THE PHYSIOLOGICAL ACTION OF TEMPERATURE

Accurate measurements of the relation between temperature and growth have been made upon roots of *Pisum sativum* (Leitch, 1916) and *Lepidum latifolium* (Talma, 1918), and seedlings of maize (Lehenbauer, 1914), also upon certain fungi (Graser, 1919; Fawcett, 1921). The curves of temperature obtained in each case are of the type shown in Figures 25 and 26, the position of the cardinal points being specific for each plant, and the form of the curve varying to some degree.

Up to the present, studies in the action of temperature have been confined too much to a consideration of the value of the van't Hoff coefficient, the so-called Q_{10}. In an endeavour to establish the validity of this rule for biological processes the numerous deviations from it have been put aside

F

too readily.   There is little doubt now that the van't Hoff
rule holds for such a restricted region of the growth curve, that
its biological value is very narrow.   From the maximum tem-
perature to the minimum the value Q_{10} decreases continuously,
only reaching in the middle regions a value of 2–3, which
the rule demands.   The temperature curve falls into four
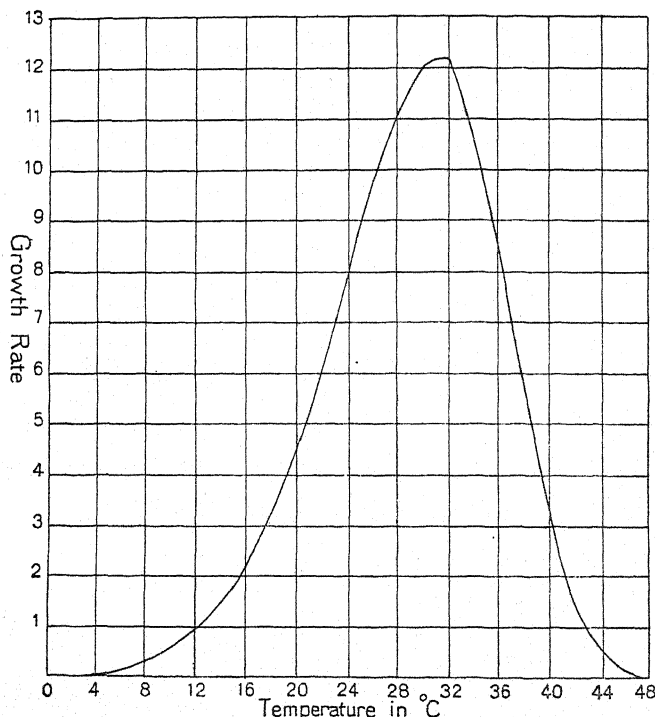principal phases, which merge into one another, viz.:

FIG. 25.—The growth of Maize seedlings at different temperatures.   (Lehenbauer.)

1.	2.	3.	4.
Low temps.	Med. temps.	Optimum	Supra-opt.
$Q_{10} > 3$	3–2	rapidly changing	< 1

The position of these phases of temperature is different
for different organisms.   Unfortunately the material so far
collected is insufficient for any far-reaching conclusions.
As an example of the differences it can be mentioned that
Phycomyces nitens (Graser) is in "phase 1" until about 7°C.,
while parasitic fungi investigated by Fawcett exhibit a Q_{10} of
between 3·1 and 6·6, even at 17° C.

THE TEMPERATURE FACTOR 67

It had been supposed by earlier workers that the position of the optimum was specific to the species (Sachs, 1887; Pfeffer, 1901–4). Determinations of the optimum temperature are very much complicated by the fact that its position is displaced according to the time of operation of the temperature (Talma, 1918; Fawcett, 1921). The profound modulation of the Q_{10} in the course of the growth period appears
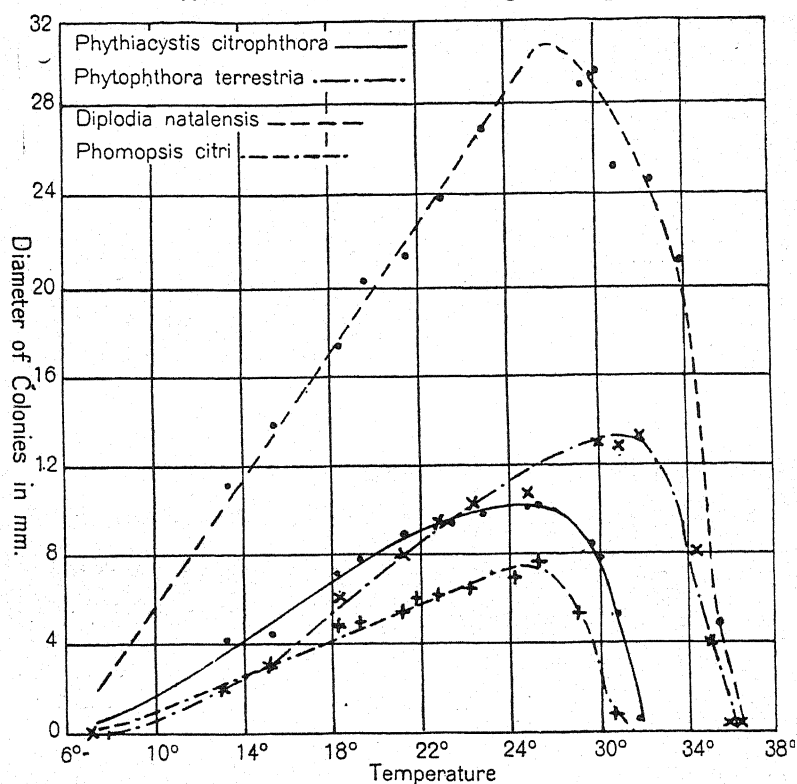

FIG. 26.—The growth of various fungi at different temperatures, measured as the increase in diameter of the colonies.

especially in Fawcett's figures. It seems that every stage of development of a plant has its own optimum temperature (Schimper, 1898; Sierp, 1920). If, therefore, the influence of temperature on some crop like corn is determined, wherein vegetative and reproductive processes are summated, an optimum at a strikingly low level is obtained. Bialoblocki (1870), for instance, exhibited a curve for rye, which had a very flat optimum between 10° and 20° C. (Fig. 27).

The position of the cardinal points is also influenced by

other factors, such as light, uptake of nutrients, and so on (Balls, 1908; Sierp, 1920). Mitscherlich (1920) has described experiments upon the influence of soil temperature upon the growth of the subaerial parts of plants. He states that the optimum yield of mustard was not reached even at a soil temperature of 31·3° C. The optimum was reached with timothy at 25·6 °C. The mean air temperature was in the first experiment 17·0° C., and in the second 20·5° C. These results suffice to show the important part which soil temperature plays in plant geography, for in shallow soils the soil temperature will often deviate very markedly from that of the air above.

It is too early yet to consider the application of the temperature-growth curve to ecological problems. Up to the present, we have not in our possession, for a single plant, the growth curve of the whole organism in various stages of its
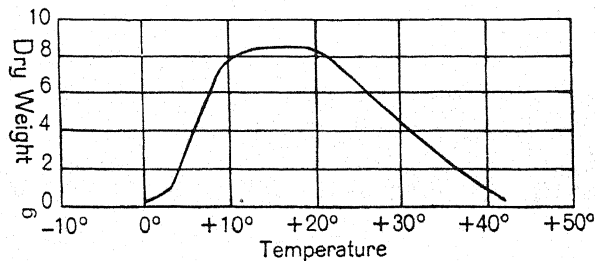
FIG. 27.—Relation between yield and temperature in rye. (After Bialoblocki.)

development, and under changing external conditions, i.e. light, water, nutrition, etc.

Summer growth, the development of storage organs, fruits, and bulbs, is naturally very closely bound up with carbohydrate assimilation. Growth in the spring depends upon assimilation less closely, for the young shoots are scarcely able to assimilate for themselves, and they draw their nourishment from stored materials in rhizomes, roots, and bulbs. In the spring, therefore, the direct action of temperature upon growth controls development, while in the summer, growth is dependent upon assimilation, which, in its turn, is controlled by temperature.

The very high temperature quotient at low temperatures means that a rise of a very few degrees reacts profoundly upon growth. To judge from the rapid development of Arctic plants in spring, their growth-temperature curve must rise very steeply in the initial phases. Plants in the Arctic

will grow when they are still standing in snow. Braun (*see*
Schröter, 1923) found *Soldanella alpina* and *S. pulsilla*
Saxifraga oppositifolia, Crocus and *Scilla bifolia* flowering
under a layer of snow a foot deep. There are many Alpines
which are able to open new leaves under the snow; for instance,
Trifolium Thalii, Luzula campestris, Pirola minor, Ajuga
pyramidalis, Gentiana Kochiana, Heiracium alpinum, and *Poten-*
tilla aurea; and even germination under the snow can take
place. Quite a number of plants grow considerably at tem-
peratures round about zero. Rubel (1922) has measured
the light intensities under layers of snow of different depths.
He has found that at a depth of ten centimetres at least 1/40
of the light penetrates, and at depths between ten and twenty
centimetres, between 1/90 and 1/3, and finally, between
fifty and eighty cm., only 1/60,000–1/2,000 of the light;
the differences being ascribed to variation in the consistency
of the snow. That the temperature relationships of growth
are bound up with those of the general activity of protoplasm,
can scarcely be doubted, although the nature of the relation
has never actually been investigated. It would be of great
interest, too, to compare the form of the temperature curves
of Arctic and Alpine plants with that of tropical plants.

One other effect of temperature cannot be altogether
neglected, namely the influence of sudden changes of tem-
perature upon the plant. As Blaauw (1908) and Graser
(1919) have pointed out, the rate of growth changes rapidly
and considerably with very small changes in temperature.
This "shock" effect of temperature, which is usually of short
duration, may or may not have much ecological importance.
It issues, at any rate, a warning that experiments carried out
at constant temperature in the laboratory, may not be com-
parable with similar experiments under natural conditions,
where the temperature of the air is always changing (Senn,
1922). In fact, the periodicity of temperature may affect the
plant just as periodicity of illumination affects it. A high
temperature by day and a high temperature by night have
an entirely different effect upon the carbohydrate balance of
the plant.   It has actually been shown by Bremer (1929) that
lettuce develops better when there is a daily rhythm of tem-
perature; night temperatures of 10°–12° and day tempera-
tures of 20°–25° C. seem to be the best.

Recently a great deal of work has been done, especially
in the United States, upon the relation between infection by

parasites and temperature. It has been found that the optimum infection temperature of *Helminthosporium sativum* is 28°–32° C. (McKinney, 1923), while that of *Tilletia tritici* lies between 9° and 12° C. (Hungerford, 1925). Leukel, in 1924, described an apparatus for the study of the action of soil temperature on plant diseases.

Two excellent publications on the relation between temperature and respiration of seedlings have been provided by the Dutch workers, Kuiper (1910) and Fernandes (1923). The respiration of foliage leaves has been studied by Kreus-
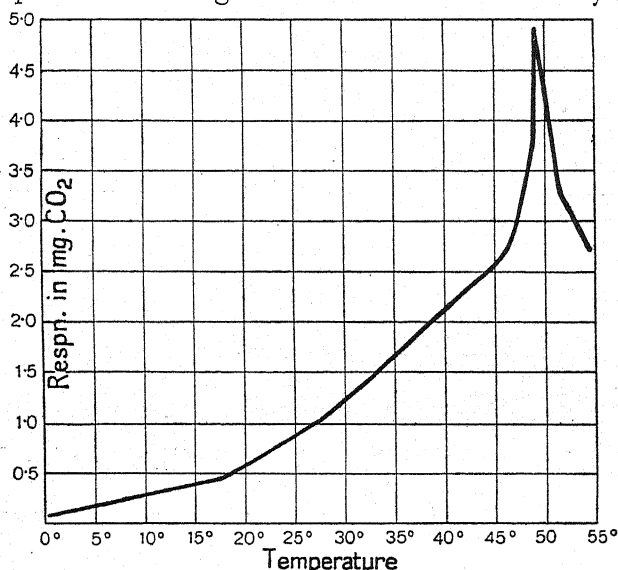
FIG. 28.—Temperature-respiration curve of leaves of *Solanum tuberosum*.

sler (1889), Matthaei (1905), Johansson (1926), and the author (1924, *f*).

All these investigations agree in showing that the curve of respiration at sub-optimal temperatures is much more regular than the corresponding growth curve. The temperature quotient for respiration remains at about the value for a chemical process, i.e. 2–3, over a much wider range in respiration curves than in growth curves. The optimum for the respiration of potato leaves lies on a sharp peak at about 50° C. (Fig. 28). Above 50° C. the curve falls very rapidly and the leaves only withstand this supra-optimal temperature for a few minutes or seconds. The time factor, observed by Kuiper, therefore, is really the expression of a pathological process, which is brought about by the high temperature.

At 40° C. the leaves remain quite fresh for four hours; only after six hours at this temperature can signs of injury be observed.   The action of this "time factor" has been discussed fully by the author (Lundegårdh, 1924, f).

Respiration is the sink into which the energy stored in carbohydrates and fats is continuously poured.   In a field of oats, for instance, the amount of carbon dioxide respired during the night reached, in a specific instance, one half of the quantity which had been combined as carbohydrate during the day.   Thus a field which produces 5,000 kilograms per hectare in stem, fruit, and leaf, has really assimilated about 10,000 kilograms of material; and fully half has been used up in respiration (Lundegårdh, 1924, a, p. 62, 259).   After allowing for the loss due to respiration, the net gain of assimilate is stored in the various newly formed storage organs of the plant, so that the respiration per unit dry weight will decrease in the course of development.   Part of this stored material is lost, so far as the effective capital of the plant is concerned, for it is converted into cellulose or into wood.   In woody plants this useless capital reaches a very high proportion.

Of the carbon dioxide balance of plants, very little is known.   It is evident that the rate of respiration, especially in a plant living close to its light minimum, will determine whether the plant is above or below the hunger limit (Lundegårdh, 1921, d, 1922, a).   In these circumstances, too, the night temperature is of great importance.   The cooler the night, the lower the loss by respiration.   Plants dwelling in shallow formations, where the nocturnal radiation is very high, respire less vigorously during the night than the dwellers in deeper formations and on the sea-shore.   To take the corn-field again as an example: The assimilation reaches about 300 kg. for a day of eight hours.   The respiration at 20° C. reaches about 175 kg.   The net yield, therefore, is about 125 kg.   Now when the night temperature sinks to 10°, the total respiration sinks to 132 kg. (12 hours at 20° C., and 12 hours at 10° C.).   The net yield is thus 168 kg., i.e. 30 per cent more than at the higher night temperature.   In actively growing plants, the matter is more complicated, owing to the fact that lowering the temperature lowers the growth as well as the respiration.   For the economy of an adult plant the cool night is certainly advantageous, so long as the temperature does not sink low enough to impair the processes of translocation.

There are some plants which have a definite adaptation resulting in a reduction of the nocturnal radiation, namely the succulents (Nicolas, 1909; Lundegårdh, 1924, *a*, p. 66). At night, they burn down their carbohydrates to intermediate substances, the various plant acids. In this process nothing is lost to the outside environment. In daylight the decomposition is completed, but the carbon dioxide formed is recombined immediately in assimilation. This narrow carbon dioxide cycle may be regarded as an adaptation against lack of carbon dioxide, which would otherwise occur among succulents, since their stomata may remain closed during the day as a protection against excessive transpiration. It is not yet known with certainty whether such an economic adaptation exists among other plants (Nicolas, 1909). The aspidistra protects itself to some extent, for, during the night, when the assimilates run low, the respiration can sink to a very low level (Geiger, 1927). Several investigators have found a marked diurnal periodicity in respiration (Johansson, 1926).

The economic advantage of the cool night holds under similar conditions for the winter period in temperate and Arctic regions. Resting buds, rhizomes, and bulbs always respire, though to a less degree than active organs. A high winter temperature, therefore, which cannot hasten development or ripening, may result in a serious loss of stored material, and jeopardize the development of the plant in the following spring. For the critical examination of these phenomena the daily range of variation of the temperature, and the mean length of the frost-free period must be known; observations of this nature, made by Hamberg (1912), are tabulated below.

TABLE VIII

Place.	Range of Variation of Temp. in July.	Number of Frost-free Days in the Year.
Inland	7·68–9·37° C.[1]	—
On the coast	6·81–7·50° C.	—
At sea	3·93–5·88° C.	—
Jämtland (inland) . .	7·23–10·66° C.	154
Stockholm (E. Coast) . .	7·85–9·38° C.	215
Hallands (W. Coast) . .	7·47–9·06° C.	242

[1] The two numbers refer to the Stations with the most extreme means.

These mean values naturally give nothing more than a schematic representation of the real relationships. In addition, the absolute temperature values are of importance and so are the daily durations of the extremes. The relation between the length of the uninterrupted frost-free period and the geographical position is of interest. Along latitude 39 N. in the United States lie Washington, with an average frost-free period of 180–210 days, Elkins, in Virginia, with 150–180 days, Colorado, with 90 days, and the Sacramento region
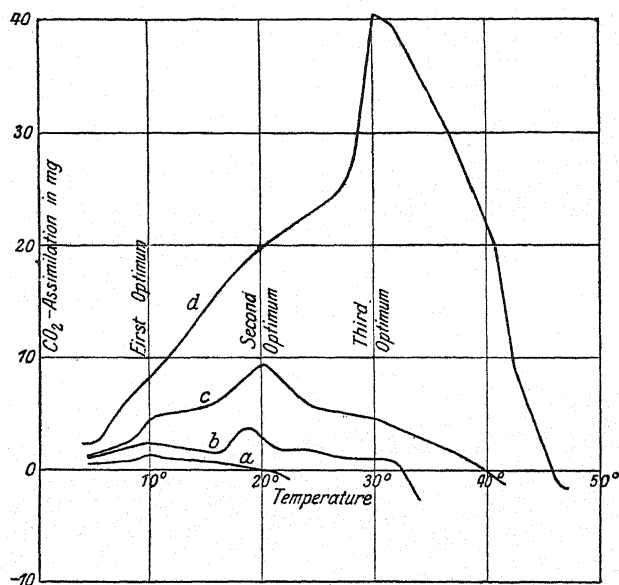
FIG. 29.—The relation between assimilation and temperature, light, and CO_2 content of the air. (a) Very weak light, and very low carbon dioxide concentration (theoretical curve); (b) 1/25 light, 0·03 per cent CO_2; (c) 1/1 light, 0·03 per cent CO_2; (d) 1/1 light, 1·22 per cent CO_2. (Lundegårdh.)

in California, where the length of the frost-free period exceeds 240 days. In the southern tip of Florida, killing frosts do not occur at all (Marvin, 1918).

The temperature curve of photosynthesis deviates markedly from that of respiration. Its form depends, among other factors, upon the intensity of the light, and the concentration of carbon dioxide in the atmosphere. The four curves in Figure 29 throw some light upon the temperature relationships of carbon assimilation, under the following conditions (Lundegårdh, 1924, f):

1. Strong light and high carbon dioxide concentration.
2. Strong light and low carbon dioxide concentration.
3. Weak light and high carbon dioxide concentration.
4. Weak light and low carbon dioxide concentration.

In the first curve d, the optimum is reached at a temperature of 30° C. This has been called the third optimum. The convexity in the curve at about 20° C. marks the position of a second optimum, which, in curve c, occurs as the highest point of the curve. This optimum appears at the same temperature in curve b, but here there is indication of a second
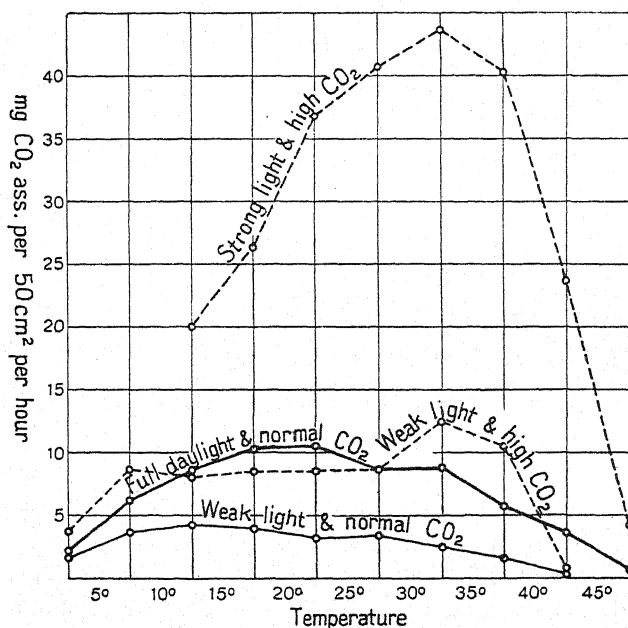
FIG. 30.—The influence of carbon dioxide and the intensity of daylight upon the assimilation of the leaves of sugar beets. (Lundegårdh, 1927.)

peak at about 10° C. Under minimal conditions, in curve a, the optimum probably occurs at 10° C.

These curves were first obtained for potatoes and tomatoes, and their form has been confirmed by experiments on sugar beets (Lundegårdh, 1927, a) (Fig. 30), *Vicia faba* (Walther, 1927), *Phaseolus vulgaris* (Yoshii, 1928) and *Hordeum vulgare* (Beljakoff, not yet published). The results differ from those of Matthaei and Blackman (1905) principally in that they show that the position of the optimum temperature

depends upon the light and the carbon dioxide concentration. The position of the optimum is, moreover, specific to the species, and may be regarded as an adaptation to the ecological conditions under which the plant lives. Thus the optimum temperature of assimilation, under normal conditions, is 18°–20° C. in the potato, while in anemone, which is a spring plant, it is only about 15° C. (Lundegårdh, 1927, *a*). In beans, the optimum is as high as 27° C. (Yoshii, 1928). The form of the temperature curve, too, may have originated as an adaptation to temperature. Sugar beets are better able to withstand extremes of temperature than are potatoes, a fact which is shown by their respective temperature curves
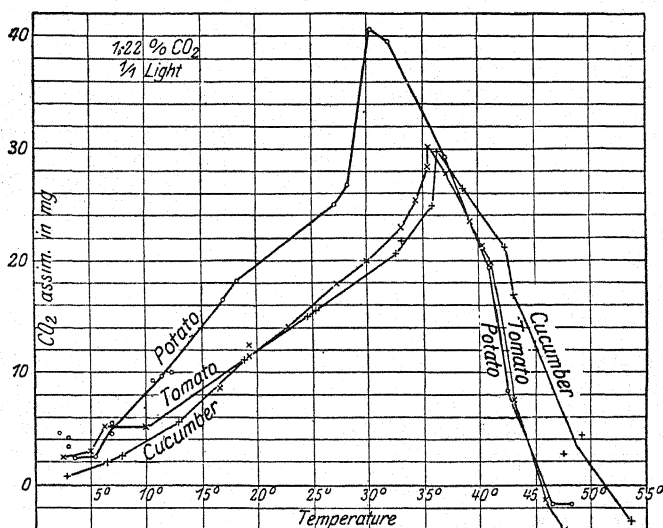
FIG. 31.—The temperature-assimilation curves of potatoes, tomatoes, and cucumbers, in 1·22 per cent CO_2 and full daylight. (Lundegårdh, 1924.)

(Fig. 31). The curve for potato rises steeply to its optimum, while that of the beet has a flat optimum between 10° and 30°. According to Stocker (1927), the lichens *Lobaria* and *Umbilicaria* have more than one optimum under any one set of conditions; these plants, therefore, will have several compensation points.

The results of these and similar experiments throw a new light upon many of the phenomena common in plant geography. The position of the "normal" optimum between 15° and 30° C. (in full sunlight and 0·30 per cent carbon dioxide) is of advantage in a temperate or cold temperate

climate, where the highest day temperature seldom exceeds 30° C. Even in the sub-Arctic the maximal day temperature often reaches 20° C. It is undoubtedly of great significance for the vegetation of the earth that many plants are able to assimilate carbon dioxide at 0° C., and that their optimum under normal conditions is between 15° and 20° C. In Tables IX and X are set out some data upon this point.

TABLE IX

THE RELATION BETWEEN ASSIMILATION AND TEMPERATURE, EXPRESSED AS MG. OF CARBON DIOXIDE PER 50 CM² PER HOUR

Temperature.	$\pm 0°$	$+10°$	20°	30°	40° C.
Potatoes . . .	0·9	4·2	9·5	4·6	Negative.
Tomatoes . . .	3·3	6·0	8·4	3·9	Negative.
Sugar beets . . .	3·0	6·0	8·5	7·0	3·8
Beans (Yoshii) . .	1·6[1]	2·3	4·6	6·5	4·8
Anemone nemorosa . .	2·8	5·5	5·2	3·2	Negative.

[1] At 3·0° C., light $\frac{1}{4}$.

TABLE X

THE EFFECT OF LIGHT AND CARBON DIOXIDE UPON THE POSITION OF THE TEMPERATURE OPTIMUM OF ASSIMILATION

Carbon Dioxide Factor	Assimilation 1/25 Light.	Optimum 1/1 Light.	Plant.
Normal (0·03%) . .	17° (10°)	20° C.	Potato
High (0·8–1·2%) . .	25	31	
Normal	—	20	Tomato
High	—	35	
Normal	12	19	Sugar beets
High	34	36	
Normal	10	18	*Vicia faba* (Walther, 1927)
Normal	24	30	*Phaseolus vulgaris* (Yoshii)
High	30	36	
Normal	± 3?	± 15	*Anemone nemorosa*

A determination of the efficiency of the assimilation at different temperatures has shown that at the normal optimum,

the relative utilization of the light is at a maximum. In this region of the curve, plants react markedly to small changes in intensity of light; so that under normal conditions, the light controls the vegetation. Between 10° and 20°, the light can separate plants into sun and shade types; below 10° the relative effect of the light is insignificant. The ratio of $\dfrac{\text{assimilation at } 1/1 \text{ light}}{\text{assimilation at } 1/25 \text{ light}}$ for potatoes and beets, between 0° C. and 10° C. is 1·3 to 1·7; between 20° C. and 25° C. it is 3·1 to 3·6. So when the prevailing temperature is below 10° C., there is no marked differentiation of the vegetation into sun and shade forms.

The distribution of algæ in the sea is also interesting in this respect. It has long been known that algæ reach a quantitative maximum in the polar regions. On the assumption that the temperature-assimilation curve of algæ resembles that of higher plants, this maximum in the cold seas is easily explained, for in weak light the maximum assimilation occurs at about 10° C. As regards their illumination, algæ are in the same position as extreme shade plants. Further observations upon water plants have recently been made by Ruttner (1927). It should be observed that the curves described above are independent of the stomatal aperture and the respiration.

For some time it has been known that many plants can still assimilate at temperatures below 0° C. Henrici (1921) has found very low temperature-assimilation optima for Alpine lichens and phanerogams, and she has established a difference in the temperature-assimilation curves of sun and shade forms of the same species (*Veronica belloides*). Alpine shade plants have, as a rule, an optimum temperature for assimilation lying between 7° and 14° C., and this is in agreement with the results obtained by Johansson (1926) at Hallands-Väderö.

Harder (1924) has given further examples of the adaptation of assimilation to the ecological factors of the habitat. Harder cultivated *Elodea, Fontanalis, Chara,* and other water plants at 4–6° C., and at 20° C. over long periods. He found that in weak light the plants cultivated at the lower temperature assimilated less at 18° C. than at 8° C., whereas the assimilation of the plants cultivated at 20° C. was greater at 18° C. than at 8° C. Under more powerful illumination assimilation is greater in both sets of plants at 18° than at 8°; but the curve of the "cold" plants rises less steeply than that of the "warm" plants. Whether three optima occur in these plants, as in

Solanum, is not known, for Harder has not yet determined intermediate points on the temperature curve. The different slopes of the two curves between 8° and 18° would indicate that in weak light there is a low optimum, a result in accordance with those of the present writer. In contrast to the earlier opinions, Harder's results indicate that the leaves of both sun and shade plants are best adapted to the assimilation conditions under which they live.

Harder's experiments were concerned with a phenotypic adaptation—sun and shade forms of the same individual; but the other examples cited above concern genotypic differences in the form of the assimilation curve, which are manifest even when the plants are growing under identical conditions.

2. The Temperature Limits of Life

The optimum region of assimilation, which has been discussed above, signifies the temperature above which the rate of carbohydrate production begins to fall, and the plant has passed its limit of greatest efficiency. This is undoubtedly of great moment in deciding the distribution of plants and in the determination of their "geographical optimum." The extreme limits of plant distribution are determined by the temperature of freezing, and the lethal temperature. Death from either of these causes can only occur when the protoplasm is irreversibly injured; a mere suspension of its functioning does not necessarily entail death. Numerous plants in the Arctic regions can withstand freezing, and resume their normal functioning upon thawing. According to Kjellmann (1885, and see Schröter, 1923), *Cochlearia fenestrata* can withstand winter conditions even when in the flowering state, and continue its development in the spring. In the Arctic there are hundreds of plants which can withstand temperatures as low as $-60°$ C., together with repeated freezing and thawing (Schimper, 1898; Kihlman 1890). Organs with low water content are known to exhibit the highest resistance. Dry seeds, for instance, will endure temperatures ranging from $-200°$ to $-258°$ C. (Bequerel, 1910; S. Arrhenius, 1906), while in the imbibed state they would be killed at a much higher temperature.

A great deal of work has been carried out upon the cold resistant capacities of different plants. While some plants will resist temperatures below zero centigrade, certain tropical plants (*Coleus, Gloxinia, Tradescantia, Begonia*, etc.) are

killed at temperatures ranging from 1·4° to 3·7° C. (Molisch, 1896); and Noack (1912) has asserted that thermophilous fungi and bacteria die at room temperature. As a cause of death by freezing it has been suggested that the intracellular formation of ice removes water from the cells, and a consequent denaturation of the protoplasm takes place (Molisch, 1897; Maximov, 1912, 1914). The mere mechanical injury to the cells may also bring about death. It is possible that cellular adaptations, such as the increase of the sugar concentration of the cells during the winter, may act as a protection against freezing (Livingston and Shreve, 1921; Åkerman, 1918, 1923; Lidforss, 1907).

An equally wide range of variation occurs with respect to the position of the lethal temperature. Alpine shade plants, for instance (Henrici, 1921), and arctic marine algæ possess very low maximum temperatures. Death in these instances cannot be due to a coagulation of the protoplasm. A disturbance of the nutritive balance is more likely to be the cause, or the upsetting of the respiration-assimilation balance. A similar crisis would arise if the potato plant were grown at too high temperatures; for the respiration increases up to 50° C., while the assimilation reaches its optimum at 20° C., and is zero at 40° C. The plant always contains some reserves of stored material, so that any harmful action due to exposure to high temperature will depend upon the time of exposure. The high but transitory maximum temperature of a continental climate is less injurious for "cold plants" than the continual "forcing house" conditions of a tropical coast climate.

Of the mechanism of heat adaptation we know less than we do of adaptation to cold. It is clear, however, that such adaptations will be correlated with the form of the temperature-assimilation curve. Where, for instance, the falling limb of the curve for cucumbers (Fig. 27) is less steep than that of the tomato curve, it could be supposed that the former can resist heat better than the latter, in spite of the fact that their optima almost coincide. The upper temperature limit, above which the ratio of assimilation to respiration falls below unity, results in starvation of the plant; and somewhere above this limit lies the point of instantaneous death, the coagulation point.

Even the point of coagulation of the protoplasm, at which instantaneous death occurs, does not seem to be very closely defined. The author observed potato leaves at 40° C. to

remain fresh and functioning in the light for four hours. After an hour at 42·5° C. the leaves were mottled with dark patches, indicative of dead tissue. Above 50° the death of the whole leaf occurred within a few minutes. It is possible that the different parts of the cell do not possess the same temperatures of coagulation. The higher the temperature is, the quicker does the irreversible change take place.

The lethal temperature can be raised or lowered by the influence of other factors. It is well known in colloid chemistry that the coagulation point can be considerably altered by the presence of salts (Pauli, 1899; Kahho, 1921). A concentration of from 0·3–0·4 normal raises the coagulation point; the most active ions in this respect are sulphate ions and chlorine ions, which raise the coagulation point of *Tradescantia zebrina* cells to between 74°–76° C.

Facts like these might account for the power desert plants have to endure extremes of heat; the salt content, especially that of the chlorides, is often considerable in these plants (Fitting, 1911; Lundegårdh, 1919, *a*).

Seeds and spores deprived of water are able to withstand very high temperatures, and this property may be of great use to plants growing in tropical deserts. Schimper, for example, has recorded temperatures ranging from 70° to 80° C. (1898). In Palestine surface temperatures of 55°–62° C. have been measured (Buxton, 1924), and in the Arizona desert temperatures as high as 71·5° C. (Sinclair, 1922). Even in Europe, dry soils, especially chalk, reach temperatures as high as 47° C. in the sun (Kraus, 1911). All these temperatures are above the lethal temperature of potato leaves.

In view of the fact that they live in water with a low salt content, the extraordinary resistance of thermophilic organisms against insolation is remarkable. The vegetation of hot springs consists almost exclusively of algæ, principally belonging to the Cyanophyceae; in addition to bacteria of various sorts. In the zones of temperature around a hot spring is found a zonation of the algæ, *Mastigocladus laminosus* from 49°–53° C., *Oscillatoria formosa* from 45°–49° C., and from 35°–40° C. *Oscillatoria princeps* (Vouk, 1923). The first species has its optimum temperature at 53° C., and its maximum at 55° C., and the last is almost "normal." The most remarkable thing is the high level of the optimum of the first species, which must necessitate a peculiar form of the assimilation curve. The minimum temperature for growth lies at

about 40° C. At room temperature, though the alga will remain alive for about a month, no growth takes place at all.

Bacteria have been observed to flourish at much higher temperatures. The hay bacillus, for instance, lives at 70° C. (Miehe, 1919) and certain other bacilli at temperatures as high as 78°–83° C. (Georgewitsch, 1910). In bacteria and fungi the position of the optimum temperature has been found to depend upon the nutritive conditions (Pfeffer, 1901).

Some attention will now be paid to the common "adaptations" against extremes of temperature. Such adaptations can be arranged into two groups: firstly those which are directly morphological or physiological, and secondly, those which depend upon a displacement in time of the developmental process.

To the first group belong those intra-cellular adaptations against freezing which have been already mentioned. Henrici's work has shown that there is range of adjustment with respect to this adaptation. She investigated the osmotic pressures of a number of plants brought for a short time to a lower temperature (Henrici, 1921; *see also* Meier, 1916). Some of Henrici's results are set out in Table XI.

TABLE XI

Plant.	Length of Exposure to Temperature.	Value of Osmotic Pressure in mol. KNO_3 at:		
		$-10°$	$0°$	$+15°$ C.
Sibbaldia procumbens				
Palisade . . .	two hours	$\frac{4}{5}$	—	$\frac{1}{4}$
Epidermis . . .	„	$\frac{1}{3}$	—	$\frac{1}{3}$
Veronica belloides				
Palisade . . .	three hours	$\frac{1}{2}$	$\frac{1}{3}$	$\frac{1}{4}$
Epidermis . . .	„	$\frac{1}{3}$	$\frac{1}{4}$	$\frac{1}{4}$

We do not know whether there is a similar plasticity of the plant with regard to heat extremes. In *Bacillus fluorescens* Dieudonné has observed an accommodation to high temperatures. (*See* Pfeffer, 1901, II, p. 91.) The usual means of protection which the plant has against insolation is to be found in its transpiration. A mesophytic leaf, with open stomata, in full sunshine is heated only to an insignificant degree (Miller and Saunders, 1923). This was ascertained by putting a

thermo-element in the leaf itself. On the other hand, other investigators have reported leaf temperatures in considerable excess of the temperature of the surrounding air (Dixon, 1924; Miller and Saunders, 1923). It is possible that the leaves investigated in these instances were not respiring normally.

Under favourable conditions the total energy of radiation reaches 1·5 gram Calories per square centimetre per minute. If we assume that the energy is completely absorbed (this is not strictly true, for part is reflected and part penetrates the leaf), then the energy represents the heat of vaporization of 2·5 milligrams of water. The transpiration value of a leaf (according to Pfeffer) lies somewhere between 0·7 and 7·0 milligrams per square centimetre per minute; a value of the same order as that suggested above (Burgerstein, 1920).

All circumstances which tend to inhibit transpiration tend to raise the temperature of those parts of the plant exposed to light, especially those parts, like leaves, in which the area is large in proportion to the volume. Miller and Saunders found that the leaves of wilting plants, in which the stomata were closed, attained a temperature 6° C. higher than that of the surrounding air. The author has found a rise of 2° C. in the temperature of cucumber leaves in closed greenhouses, where the air was saturated. In bright diffuse light, however, the transpiration is almost enough to reduce the temperature to as much below that of the air (Lundegårdh, 1924, a; Willstätter and Stoll, 1918).

Owing to the frequent danger of water shortage and wilting, the plant has great need for various protective arrangements against radiation; and such arrangements do, in fact, occur in great variety: oblique orientation of the leaves, the covering of the leaves with white protective hairs, the light colour (see Stahl, 1909), the paucity of chlorophyll in sun plants, the ability of the chloroplasts to assume a profile position (Senn,[1] 1908) and factors like reduction of surface, and the resistance of the various organs to desiccation.

Unfortunately the physiological investigation of these adaptations has lagged behind the morphological description of them. As a rule, interpretation has gone no further than to offer an elementary and obvious physical explanation. It would be of the greatest interest and importance, for instance, to ascertain just how satisfactory as a defence poverty in chlorophyll is, and to what measure it protects the plant under

[1] (*Eie Gestalts u. Lageveränderung der Pflanzenchromatophoren,* 1908.) ED.

a given set of environmental conditions.   It is only very rarely that the air temperature reaches supra-maximal values. Temperatures as high as 50° C. have been reported only in isolated instances (Schimper, 1898).   In a high temperature of short duration the succulents are at an advantage, for it is some time before the whole body of the plant is warmed up.

The very periodicity of temperature is a factor of some importance in the study of its ecological significance, and it is impressed upon the plant life itself.   The occurrence of a latent stage in the life-history of a flowering plant, a stage which can better withstand winter than the actively growing stage, enables plants to flourish at greater heights and farther north than would otherwise be the case.   Seeds, buds, rhizomes, bulbs, etc., are protected by virtue of their poverty of water, their chemico-physical methods of ensuring a low freezing-point, and their situation under the ground or the snow.   The more severe a climate is, and the more marked its yearly fluctuation of temperature, and water supply, the more frequently are species with efficient resting organs found. This has been the subject of thorough investigation by Raunkiaer (1918); this author has made the basis of his phytogeographical system the position of the vegetative "latent" organs with reference to the soil.   He distinguishes (Fig. 32):

1. *Phanerophytes*, with overwintering buds, and branches standing high above the earth.   Trees and bushes, and certain epiphytes and stem succulents belong to this class.

2. *Chamaephytes*, with buds near the surface of the soil. To this class belong low bushes, and certain shrubs, like *Stellaria holostea*, and species of *Sedum*.

3. *Hemicryptophytes*, with buds closely over or under the soil surface, and which are protected by soil or the remains of leaves.

4. *Cryptophytes*, with buds under the earth; including geophytes, with creeping runners or rhizomes, bulbs, corms, etc.; also water and bog plants.

5. *Therophytes*, or annuals, which overwinter by seeds.

Raunkiaer finds a certain specificity of life form to climate, though it does not follow that all the species in one climate belong to the same life form.   The frequencies, expressed as percentages, of the life forms, Raunkiaer calls the "biologic spectrum" of the region in question.   In Table XII a few of Raunkiaer's "spectra" are set out (*see also* Fig. 32).

xeromorphism, cannot always be considered as adaptations to the ecological factors which were first thought to act upon them; and that the same external life form, which in the one instance is a very important protective device, in another is something quite secondary, and of no particular importance. The same research has revealed, in some cases, a marvellously fine "fitness" in the organization of plants.   This outlook of experimental ecology has, of course, nothing to do with that teleology coloured with anthropomorphic ideas so common a decade ago.   When one speaks of adaptation, for instance, one does not refer to a "Lamarkian" idea of adaptation.   To say, for instance, that a shade plant is "adapted" to life in the shade, signifies that on account of its genotypic "make up," the organization of such a plant will only reach its optimum under these conditions.   Certain genotypic characters play a greater part in competition than others, and it is the function of experimental ecology to discover and to analyse these "prevailing" adaptations.

3. Temperature and Rate of Uptake of Salts

A change of temperature affects every process in the living plant; some space must now be devoted to secondary processes in the plant as they are influenced by temperature; and the first of these to be considered is permeability, which determines the rate of uptake of salts through the roots. (*See* Fig. 33.)

Rysselberghe (1901) found that tissues recover from plasmolysis seven times quicker at 20° C. than at 0° C.   According to Delf (1916), the permeability to water increases with increasing temperature up to 42° C.   The temperature relationships of permeability have been fully worked out by Ursprung and Blum (1921), by Stiles and Jörgensen (1917), and also by Bode (1923) (Fig. 33).   Dixon (1924) has worked upon the permeability of leaves; he found that between 10° and 30° C. the value was doubled, and at 20° C. it was 50 per cent higher than at 10° C.   This increase in permeability might explain the damage done to leaves by heating.

Although there have been very few purely physiological investigations of the action of temperature upon the uptake of salts, yet it seems very probable that changes in permeability induced by temperature changes play an important part in the

life of the plant. The temperature of the soil is important in this respect. The relation between soil temperature and air temperature has been given by Kraus (1911) and certain of his results are represented graphically in Figure 34. It is evident that the two do not always run parallel.

In extreme cases a low soil temperature can endanger the life of the plant, for the roots can take very little water from a frozen soil (Kosaroff, 1897). On this account there are some Arctic regions, where, although the air temperature is high enough to support life, the soil temperature is too cold to
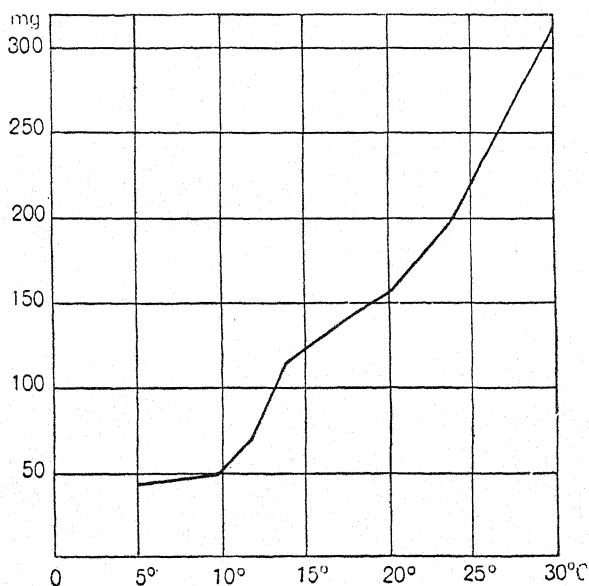
FIG. 33.—Change of permeability in the root of *Helianthus annuus* with increasing temperature. (After Bode.)

admit of the growth of higher plants. Even in more temperate regions the soil temperature is a factor which has to be reckoned with. The roots of trees are too deep, as a rule, to be frozen, and those of very shallow-rooted plants thaw rapidly in the spring; but roots at a depth of two to three feet may sometimes suffer seriously.

As an integral part of the local climate, the soil temperature is of very great significance; a significance which is in part direct, since it influences the uptake of salts, and in part indirect, since it determines to some extent the local air temperature. This indirect effect is of some importance in

localities where wind is not prevalent.   The temperature of
the soil surface depends upon the intensity of the sunlight, upon
the physical texture of the soil, and upon the nocturnal radia-
tion.   Observations upon the relation between heating and
texture of soil have been given by Ramann (1911) and others.
Shallow soil formations, especially when they are open, exhibit
higher day temperatures and lower night temperatures than
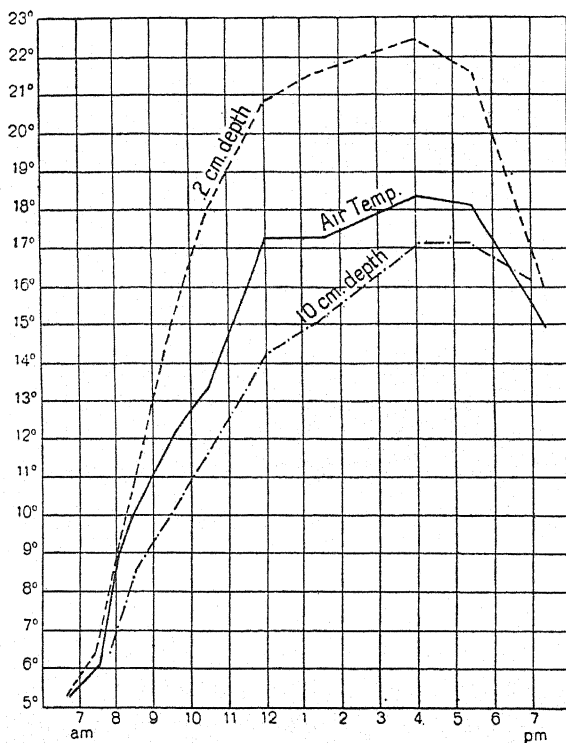
FIG. 34.—Daily course of temperature in the air and in the open soil at Wurzburg,
April 23.   (After Kraus, 1911.)

deep formations.   The differences between the temperature
climate of a wood and of the open have been discussed by
Salisbury (1916), Schröter (1923), Larsen (1922) and others.
The temperature climate of a wood is much cooler in summer
and somewhat warmer in winter, than the corresponding
climate in the open, and in addition the time of day at which
the maxima and minima occur differ in the two habitats
(Lundegårdh, 1921).   Some data on this point are set out in
Table XIV.

TABLE XIV. (After Lundegårdh)

TEMPERATURE DIFFERENCES BETWEEN WOOD AND MEADOW, IN NEIGHBOURING HABITATS (ABOUT 400 YARDS APART). THE SUMMER WAS RAINY AND COOL. 1918.

Month.	Wood.				Meadow (near Seashore).			
	Time a.m.	Min. Temp.	Time p.m.	Min. Temp.	Time a.m.	Min. Temp.	Time p.m.	Min. Temp.
June . .	5·00	9·0°	2·30	13·3°	5·00	9·0°	1·25	20·4°
July . .	5·00	11·0°	3·25	14·3°	4·45	12·1°	2·25	21·4°

In open habitats the temperature of the soil may be several degrees higher than that of the air above (*see* Keen and Russell, 1921). Kraus (1911) has recorded very high temperatures in the chalk. Some of his results are tabulated in Table XV.

TABLE XV

MAXIMUM SOIL TEMPERATURE IN THE CHALK AND IN THE BOTANIC GARDEN AT WURZBURG

Place.	Depth cm.	Time.	Air Temp. ° C.	Soil Temp. ° C.	Difference.
CHALK.					
Beside *Festuca ovina* .	2	11·30	26·0	42·0	16·0
Among *Stipa capillata* .	2	1·35	22·4	38·5	16·1
Beside a bush of *Euphorbia*					
gerardiana . . .	2	2·00	31·0	42·5	11·5
BOTANIC GARDEN.					
	2	2·45	27·5	42·0	19·5
	10	2·45	27·5	34·0	6·5

According to Kraus, these high soil temperatures are not exceptional, but occur fairly commonly, and his work is supported by the more recent observations of Stocker (1923). Since the intensity of radiation increases with the diathermy of the atmosphere, this effect might be expected to increase with height above sea-level; this is, indeed, actually the case (Schröter, 1923). An interesting example is given by Maurer. At a height of 9,000 feet the soil at a depth of fsur

feet was 2·9° warmer than the air. At 1,800 feet, the difference was only 0·5° C. There seem to be no observations published upon the temperature of surface layers of soils in the Alps; one would expect still bigger differences between air temperature and soil temperature than are recorded by Kraus.

The heating of the soil depends, too, upon the layer of vegetation covering it. According to Wetter (quoted by Schröter, 1923), a rapid rise of temperature occurs in soils covered with *Sempervivum montanum*, *Sedum mite*, and *Sedum annuum*, whereas with a covering of *Saxifraga aspera*, *S. Aizoon*, *Silene acaulis*, and *Festuca varia*, the heating effect is much smaller. This depends partly upon the intensity of transpiration, and partly upon the constitution of the soil, especially upon its water content.

The direction which a habitat faces, as already mentioned in Chapter II, has a great influence upon the climate of that habitat, owing to the differences in the soil temperature due to insolation. In Hann's *Handbuch der Klimatologie* the author has said: "The sunny and the shady side of a mountain exhibit enormous contrasts at very close quarters. In early spring, when the southern side is fresh and green, the northern side presents the appearance of deep winter. In late summer, though the corn is ripe and yellow on the southern side, the northern side is covered with conifers." Kerner has measured the soil temperature at a depth of 80 cm., and has found, among other results, that at an altitude of 1,800 feet, the sunny side of a mountain had an average temperature 4° C. higher than the northern side. The classical example has been given by Schröter (1923); in the Findelen valley, in Valais, rye grows to an elevation of 2,100 metres on the southern slopes. Above the rye grow fine-leaved steppe grasses, *Festuca valesiaca*, *Poa bulbosa*, open turf, and sundry herbs; "and in the neighbourhood, on the northern slope, the ground is covered by the Siberian alder, and in the little glades between an Arctic-Alpine tundra of dwarf shrub: a contrast within one kilometre equal to thirty or forty degrees of latitude."

No less striking is the influence of the exposure of the slope upon the height of the tree level; the tree line generally lies at least 300 feet higher on the south than on the north side. Since the shade temperature decreases with height, and the sun temperature increases, this phenomenon is very marked in high mountain regions (Schröter, 1923). The same is true of

mountains in the tropics. On the western peak of Kilimanjaro, at an altitude of 16,000 feet, the temperature was 70° in the sun, and 8° in the shade. At night the temperature sank to — 15°.

In the lowlands temperature is not so often a limiting factor as it is in the mountains. Any influence due to the direction which a habitat faces is therefore less pronounced. But in the researches reported by Kraus (1911) there is a definite influence due to the integrated effects of water and temperature, in chalky soils. Kraus observed that as a general rule xerophytism and nanism were more common on the south and south-west sides of many open formations, while on the north side there prevailed a closed formation with definitely mesophytic vegetation. The following example will illustrate Kraus' work:

10.15 a.m. May 27, 1903.

Northern Slope. Vegetation: green, with occasional flowers of *Poterium* and *Cerastium arvense*.
Temperature: air, 21° C.
soil, 4 cm. deep 14° C.
„ 8 „ „ 14° C.

Southern Slope. Vegetation: flowers of *Salvia, Poterium, Ranunculus bulbosus, Isatis, Hippocrepis, Dianthus*.
Temperature: air, 21° C.
soil, 4 cm. deep 29° C.
„ 8 „ „ 24° C.

The northern side was damp, and the southern side dry.

Even on railway embankments (Hesselmann, 1904), and rocks, the direction which the habitat faces can influence the vegetation; though how much of this influence is due to temperature, and how much to water conditions and illumination, is a matter which must await investigation. A high soil temperature and a low water content is to be expected in habitats with open vegetation. In closed formations, such as woods, the soil is protected from direct insolation, and the heat absorbed by the plants is used in transpiration.

From the foregoing it can be concluded that so far as the temperature climate is concerned, the measurements of meteorology are insufficient for ecological purposes. Knowledge of the mean temperature above the vegetation does not necessarily give any idea of the temperature around the shoot

and root of the plant; and even in the same habitat several temperature climates can obtain. Deeply penetrating roots, for instance, live in an entirely different temperature from shallow roots; and a tall plant lives under conditions quite different from a low one (Vallin, 1925).

4. Temperature as a Factor in Plant Geography

The unravelling of the interrelationship between the temperature climate and the distribution of plants over the earth is an old problem in plant geography; and although a vast amount of effort has been applied to its solution, very little progress has been made. Beside light and water, the temperature factor plays a great part in the zonal distribution of vegetation. Even a superficial observer would recognize that a tropical rain forest, a temperate deciduous forest, and a sub-Arctic coniferous forest are geographical entities determined by the zonal distribution of temperature over the earth. But from the superficial recognition of this relationship to its rigorous proof is a very great step.

In 1874 de Candolle made some attempt to define exactly zones of temperature. He divided the earth into five temperate zones: (1) The "megathermic" zone (mean temperature about 25° C.). (2) The "xerophilic" zone, and (3) the "mesothermic" zone (annual mean temperature about 15° C. to 20° C.). (4) The "micro-thermic" (mean temperature from 0° C. to 14° C.), and (5) the "hekistothermic" zones (in which latter zone the temperature for most months of the year is below zero, and during the vegetation period does not rise above 5° C.). De Candolle's results are unsatisfactory, however, because he neglected the changes of climate during the year.

Köppen (1884) has improved upon this classification. He defines, for example, a cold zone—a region which has for at least one month, and at most four months, a mean temperature above 10° C. In a subsequent elaboration of his method, Köppen (1900, 1918, 1923) defines the megathermic zone as the isotherm for 18° C. in the coldest month of the year; and the mesothermic zone is given by the isotherm for 22° C. in the warmest month of the year.

A correlation between the height of the tree line in the Swiss Alps and the temperature has been recorded by Quervain (1903); he found that the height of the tree-level is parallel with that of the isotherm of the mean monthly midday tempera-

ture. A certain parallelism also exists between the July isotherm for 10° C., and the tree line of the Alps (Brockmann-Jerosch, 1927). The results of this investigation are illustrated in Figure 35. A full discussion of the influence of environment upon the height of the tree line in the Alps has been given by Schröter (1923, p. 43). Salisbury (1926) has described a similar correlation between the distribution of *Rubia peregrina* and the 4·5° C. January isotherm.

Merriam (1894) and other authors have integrated the heat for the whole year or for some part of it, by methods similar to those used for the summation of light, mentioned in Chapter II. As an estimate of the temperature climate this method has serious objections. It has been improved by
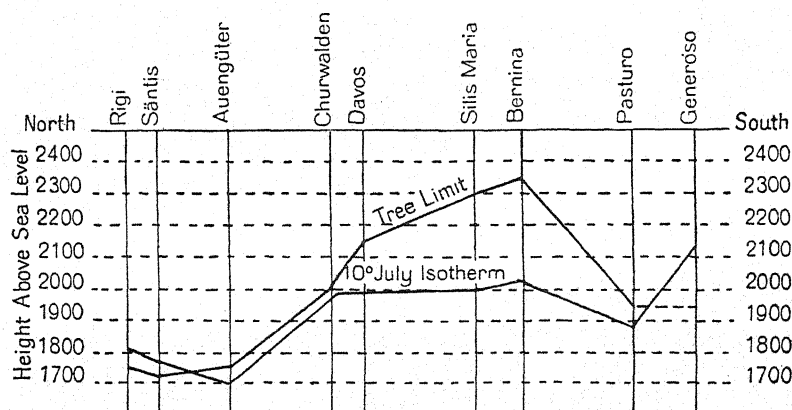
FIG. 35.—The 10° July isotherm and the tree limit. Cross-section across Switzerland. Height in metres. (Brockmann-Jerosch, 1919.)

Livingston and Shreve (1921), who estimate the length of the frost-free period, and proceed to summate the heat within this period. They determine also the number of days on which the temperature exceeds a certain value. Vahl (1911) used the mean temperature in the coldest month, k, and in the warmest month, v, and enunciated the following formula, $v = a + bk$, where a and b are constants. In this way he obtained a satisfactory temperature correlation for the northern limit of pastures in Europe and Siberia. Samuelsson (1915) has used the same formula; he took the mean temperature of the warmest month as v, and the number of days with a mean temperature greater than zero as k.

Enquist (1924) considered only the daily maxima and minima of temperature. He pointed out that the maximum

temperatures on a certain number of days exceeded a certain "mean maximum," and the minimum temperatures on a certain number of days fell below a certain "mean minimum"; and on other days the maxima and minima did not fall outside these limits. In this way he determined two limits of heat and two limits of cold. For *Ilex aquifolium*, *Fagus sylvatica*, and *Pinus montana*, Enquist obtained a good agreement between the temperature curves and the limits of distribution. These methods, which aim at correlating the temperature of a climate with the vegetation, are open to a great many sources of error. Correlations between temperature and boundaries of vegetation are probably only reliable when the temperature is a "limiting factor."

The methods of experimental ecology point another way to the solution of this problem of the influence of the temperature factor upon plant distribution. We have already seen how the action of temperature influences the fundamental processes of plant growth; only when the problem is regarded from a physiological standpoint is there any hope of separating the temperature factor from the other ecological factors. It is clear that the quantitative information given by temperature curves will enable one to determine not only the limits of distribution of a species, but also the temperature optimum of the species, a matter of great importance in ecological research. Livingston and Shreve (1921) have already begun to work in this direction, by attempting to define climatic zones on a basis of the temperature curves of growth. They have met with little success, but this is scarcely surprising, since temperature is only one of the plexus of factors which compose the climate of a region.

Examples have been cited above of the temperature curves of growth, assimilation, and respiration. Given, therefore, the temperature of a habitat, it would be possible to read off on the graphs the level of intensity of these various factors. But the question immediately arises as to whether these three processes are manifest to the same relative degree throughout the life of the plant. With growth and with assimilation this is certainly not the case; and Briggs, Kidd and West have shown (1920) that the relative respiration rate changes through the life cycle. With most green plants, especially perennials, there is a pronounced growth phase at the beginning of the vegetative period. Not until the growth of the shoot and leaves has diminished, does the full intensity of assimilation

begin; while the respiration, in spite of incidental changes, continues throughout the whole period. Since respiration supplies the energy for the various vital processes, it can be assumed that the rate of respiration increases with rate of growth. However, the "economic co-efficient": rate of growth/rate of respiration, does not always remain constant. A change in this coefficient has been observed in both higher and lower plants (Pringsheim, 1914; Lundegårdh, 1924, *a*, p. 58).

Although they occur at different times, the growth phase and the assimilation period are not independent of each other. In fact the assimilation in one year influences the growth in the next, since it is then that the stored material is used. The thickness of the annual rings, and the length of the vessels in the wood, has been found to depend upon the output of assimilate in the previous year (Lundegårdh, 1916, *a*; Douglas, 1919; Clements, 1921). Growth in the spring is also influenced by a high winter temperature, and by high night temperatures, both of which result in a certain "waste" of assimilate. The growth rate determines indirectly the amount of photosynthesis, since upon growth depends the total assimilating surface. A cold wind at the time the leaves are unfolding may cause incalculable damage as regards the amount of assimilate produced in the following summer.

In measuring temperature for the purposes of ecology, it is of great importance that the measurements be taken frequently, so that some idea may be gained of the daily march of temperature. If the curves of the most important physiological processes increased regularly with temperature, it would be possible to make use of heat summations and mean values in ecological experiments; but we know that growth curves and respiration curves do not rise regularly with temperature, and that the assimilation curve, in some instances, at any rate, has passed its optimum at 20° C. A variation in temperature of one degree, therefore, has very different effects over different parts of the temperature scale, a fact which is strikingly illustrated by the values for the temperature coefficient of respiration and assimilation in potato leaves, set out in Table XI (Lundegårdh, 1924, *f*).

Thus, at 5° C., a rise in temperature of one degree has a much more profound effect upon assimilation than a similar rise at 15° C.; and at 25° C. the same increase in temperature has a negative effect. If mean temperatures or summated

TABLE XVI

Temperature.	5°	10°	15°	20°	25°	30°	35°	40°	45°	49° C.
Q_{10} respiration	1·08	1·08	1·06	1·10	1·07	1·07	1·06	1·29	1·01	1·46
Q_{10} assimilation:										
1/1 light	1·27	1·25	1·08	1·08[1]	0·96	0·92	0·81	—	—	—
1/25 light	1·18	0·95	0·90	1·52[2]	0·79	1·00	—	—	—	—

[1] Between 18° C. and 17° C., curve *c* in Fig. 29.
[2] Between 20° C. and 19° C., curve *b* in Fig. 29.

temperatures are used in ecological calculations, the inter-relation of temperature and assimilation is simply ignored; in the same way, the maxima and minima, which are of great importance in the distribution of vegetation, are not taken into account in calculations depending upon mean temperature or summations of temperature.

The length of the frost-free period is the time from the last night frost in spring to the first night frost in autumn. American workers have recognized the great significance of this period, and have devoted considerable attention to it (Day, 1911; Livingston and Shreve, 1921). For further information the reader is referred to these authors.

The two main processes which are carried on in the plant during the night are respiration and the translocation of assimilates. It has already been shown that a considerable loss of material may occur on account of nocturnal respiration, though some is undoubtedly used in actual growth in size of the plant. Some idea of the loss through nocturnal respiration at different temperatures, in a field of potatoes, can be obtained from the following table:

TABLE XVII
Fresh weight per acre, 6,000 kg.
Leaf area per acre, 10,000 sq. metres.

Temperature in ° C.	0°	5°	10°	15°	20°	25°
Respiration per hour per m² leaf surface	0·018	0·04	0·06	0·08	0·12	0·18 gm.
Respiration per hour per acre	0·18	0·40	0·60	0·80	1·2	1·8 kg.

According to Pfeffer (1904) "there exists in the plant no marked tendency for growth . . . to take place principally in the night time." However, growth has been shown to take place during the night, sometimes even more than during the day. According to the work of Sachs (1872) and Baranetzky (1879), the maximum growth in length of flowering plants, at any rate, occurs in the early hours of the morning (Fig. 36). There is more growth between 6 a.m. and 6 p.m. than there is between 6 p.m. and 6 a.m. The position of the
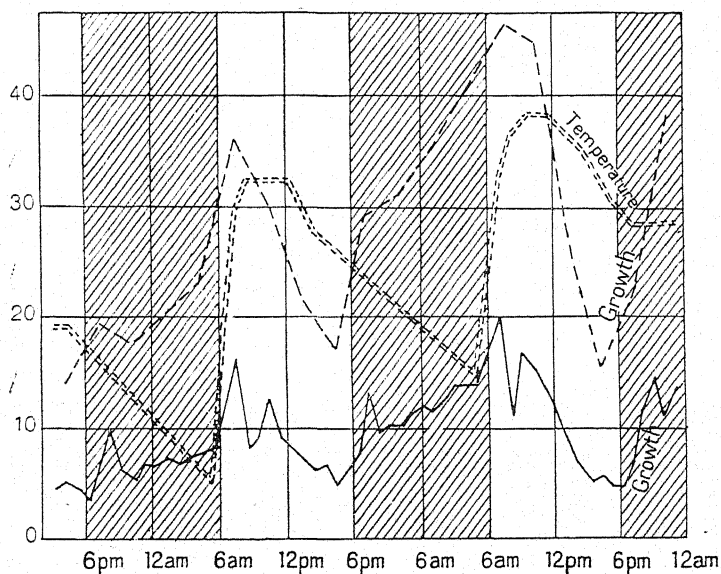
FIG. 36.—Growth movements in a stem of *Dahlia variabilis*. The upper curve represents three-hourly measurements, and the lower curve hourly measurements. (Sachs, 1874.)

maximum differs so much for different plants, that no generalization can be made. The causes behind this daily periodicity of growth are complex, and have not yet been analysed. It does not depend solely upon temperature, for growth sometimes increases during the night, when the temperature has fallen (Fig. 36). The stimulation of light, the course of assimilation and transpiration, are also factors which probably play a part. Enough has been said to emphasize the great difficulties in the way of evaluating the temperature growth curve for ecological purposes. Some idea of the differences between plants will be obtained from the following table:

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TABLE XVIII. (Pfeffer.)

Plant.					Min. Temp.	Opt. Temp.	Max. Temp.
Triticum vulgare	.	.	.	.	0°	29°	42°
Acer platanoides	.	.	.	.	7°–8°	24°	26°
Cucumis sativus	.	.	.	.	15°–18°	31°–37°	44°–50°
Zea mays	.	.	.	.	9°	34°	46°

Most of the figures refer to seedlings.

During the day the assimilation of carbon dioxide is the dominant process taking place in the plant. In a sun plant, an increase of temperature to 15°–30° C. will increase the assimilation; and further increase of temperature above the optimum will cause a decrease in the assimilation. Now a combination of the temperature curve of the habitat with the temperature-assimilation curve will give an idea of the "ideal" course of formation of carbohydrate; though it should never be forgotten that other factors beside temperature will influence the plant. By taking the daily maxima and minima of temperature, and combining these with the information from the temperature – assimilation curve, some idea of the gross assimilation can be obtained.

FIG. 37.—Maximum and minimum assimilation (the latter as dotted line) of four regions in Sweden, calculated from their temperature climates. Malmö, 55° 35′ N.; Stockholm, 59° 20′ N.; Hörnösand, 62° 35′ N.; Gellivara, 67° 10′ N. (Lundegårdh, 1928.)

In Figure 37 are represented the maximum and minimum assimilations of potatoes and sugar beets, throughout the seasons 1921 – 25, at five different localities in Sweden, calculated by the method outlined above (Lundegårdh, 1928). Of particular interest is the fact that the northern regions are more suitable for assimilation in July than Malmö in the south, for at Malmö

the maximum temperatures are above the optimum for assimilation.

A more complete picture of the relation between assimilation and climate will be obtained if the influence of the light factor is also taken into account. From the light curves of different places, and the light-assimilation curves of the plants in question, a similar series of "ideal" assimilation curves will be obtained. Such a series for potatoes is illustrated in Figure 38. In both these diagrams account has been taken of the length of the frost-free period. It has been assumed
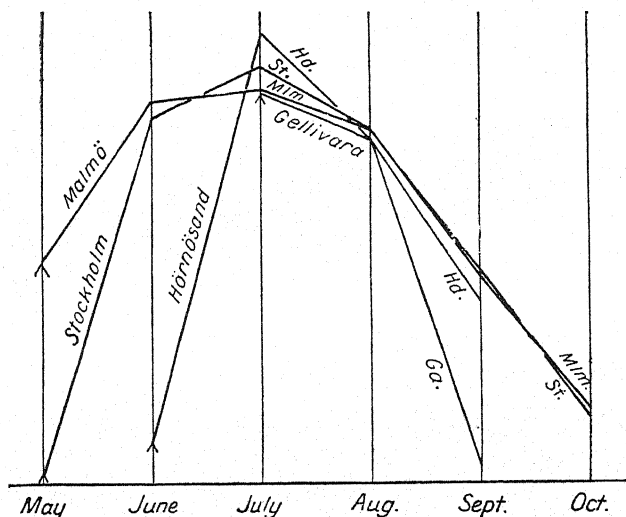
FIG. 38.—Assimilation climate of the same four regions depicted in Fig. 37, taking into account, beside temperature, the light climate, and the length of the vegetative period. The sign ∧ denotes the beginning of the vegetative period. (Lundegårdh, 1928.)

that assimilation would begin 30 days after the last frost in spring, and would end at the first frost in autumn.

This investigation has aimed at giving a first survey of the assimilation climate of Sweden, and the climate might be summarized as follows:

Southern Sweden (Malmö) has a long and equable assimilation period, conditions being particularly favourable in the spring. Further northward the spring climate becomes less and less favourable, on account of the limiting action of temperature.

Although the southern regions ($55°–59°$ N.) have the best spring climate, the region of Hörnösand ($62° 35'$ N.) has a more favourable assimilation climate in summer, the assimila-

tion curves being 12 per cent above the corresponding values for Malmö. This has already been attributed to the supra-optimal temperature at Malmö. In August the whole of Sweden has the same assimilation climate. From the ecological standpoint the autumn climate is even more equable than the spring climate.

Enough has been said to demonstrate how it is possible to combine the results of experimental ecology with data on the climate, in order to obtain a method of evaluation of the climate from the point of view of the vegetation. There is no doubt that the assimilation rate of the plant reflects its general development and growth. It is reserved for further investigations to extend this method to other crops and other climates.

On account of the relatively low temperature optimum of assimilation, the colder zones of the world are in this respect most favourable for plant life; the distribution of illumination throughout the growing season contributes to the same effect. If this relationship is general, then the "zone of highest production of assimilate" per unit assimilating surface and unit light, would not be upon the Equator but at somewhat higher latitudes. The luxuriant vegetation of a tropical rain forest depends in the first place upon the optimal water supply, and upon the fact that there is no marked periodicity of the climate to interrupt the course of growth. It would be of the greatest interest to know how high the monthly production of assimilate is in a tropical rain forest, compared with that of a deciduous temperate forest in July. No conclusions can be drawn from the data at present available. A factor which must benefit especially the ground-vegetation of a tropical forest is the carbon dioxide concentration of the air, which is much higher than the corresponding concentration in cooler zones, owing to the intense activity of soil bacteria. The temperature curve of bacterial activity, like that of respiration, does not reach its maximum until between $30°$ and $40°$ C.

In agreement with these discoveries upon the rate of assimilation, it has been observed that corn and potatoes in Central Europe and South Scandinavia produce higher yields than the same crops in the tropics (Schroeder, 1919). Many other factors beside temperature, of course, play a part in this, so that very little weight can be attached to such results; but it would be of interest to know whether the different temperature relationships of different cultivated plants depend upon differences in their assimilative capacities, or upon specific

requirements related to the vegetative periods. Probably these assimilation curves will yield valuable information as to the best temperature-climate for the optimal yield of any particular crop. Beljakoff, in the writer's laboratory, finds wide differences in the assimilation curves of two races of Barley ("Gullkorn" and "Vegakorn"), which are distinctly related to the climatic optima of the two races.

Of special claim to interest are the "autumn plants," such as *Lonicera*, certain species of rose, *Plantago*, *Bellis*, etc., and certain species of grasses, which continue to live and even to grow into the late autumn and early winter. In a mild winter these plants retain their green colour, and their development is only brought to an end by the sharp night frosts. A critical investigation of the assimilation and respiration of these plants would be of great interest. It is significant that they grow most luxuriantly in a maritime climate, where the winter frosts are longest delayed.

Growing plants need not only a definite length of the frost-free period for their development, but in addition, a certain level of temperature within that period. The findings of horticulturists indicate that the temperature optimum is shifted in the course of development (Schimper, 1898). It seems to be generally true that the "cardinal points" for the several growth and developmental processes do not coincide (Pfeffer, 1904). Thus the temperature limits of germination usually lie lower than those of vegetative growth. The formation of propagative parts, too, is often favoured by low temperature. There exists a similar divergence for the metabolic processes, some of which, the maturing of seeds and buds, for example, are favoured by low temperature.

The careful investigations of Blaauw, on the hyacinth (1924), afford an example of the profound effect of the temperature factor upon development. Blaauw put bulbs of the hyacinth at eleven different temperatures for periods varying from three to twelve weeks; forty-four combinations of temperature and time. Subsequently the bulbs were planted out in garden beds. The results were surprising in that the temperature for optimum development was higher for the first week than for subsequent weeks; the optimum sank from 23°–28° C. (in the first week) to 17°–20° C. The best development occurred after eight weeks at 25·5° C. and four weeks at 17° C. Thus the final optimum agreed roughly with the assimilation optimum already found for potatoes.

The "ecological optimum," therefore, is not realized under constant conditions, but corresponds to a climate *type*, in which the various stages of development take place under varying phases of the climate.   One is brought to this conclusion, too, from reading the valuable works of Klebs, the *Bedingungen der Fortpflanzung* (1896); according to Klebs, constant conditions favour a continued vegetative development.

A casual survey of the plant kingdom reveals an unmistakable preponderance of species which are "adapted" to periodic changes in climate.   Even in the tropics there is some correlation between time of flowering and the dry season (Schimper, 1898).   In a rain forest, which is a sort of forcing house, the periodicity is reduced to a minimum; but in spite of this, the development goes on in fits and starts, as though the tendency toward periodicity were present.   The enormous variety of forms which flourish in the temperate zones and in the Arctic, and which are so excellently adapted to the climate, are convincing evidence of the perfection which the genotypic constitution of protoplasm has attained, in its ability to change from the latent to the vital condition, an ability upon which their very presence in such a climate depends.

5. THE TEMPERATURE CLIMATE OF THE EARTH [1]

The mean temperature of the air decreases from the Equator toward the poles, at first gradually, then more
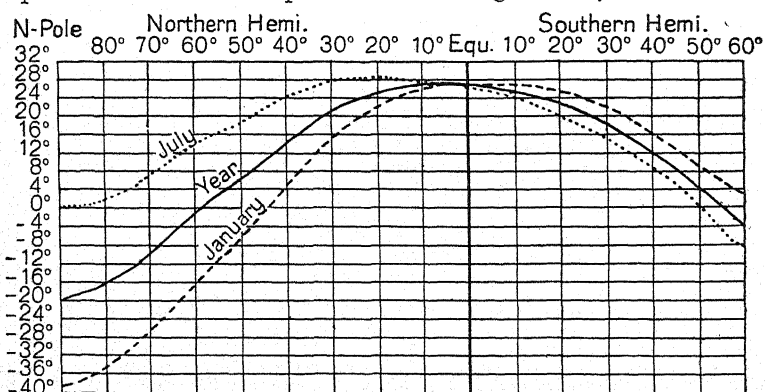
FIG. 39.—The distribution of temperature over the Earth.   (Hann.)

rapidly up to a latitude of 70° north, and then more gradually again to the North Pole.   South of the Equator the decrease

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[1] This subject has been ably discussed by Hann (1915) and Köppen (1923), so that a very brief outline will suffice here.

is at first more gradual; and beyond 60° south the decrease is very rapid (Fig. 39). The southern hemisphere is about 1·5° C. colder than the northern hemisphere.

In comparing the differences of climate caused by differences in latitude, one must take into account the course of temperature throughout the year, as it is expressed in the means for the successive months. These means are set out in Table XIX from the data of Hann.

TABLE XIX

MEAN MONTHLY TEMPERATURE IN ° C. OF VARIOUS REGIONS

Place.	Latitude.	Jan.	Feb.	Mar.	April.	May.	June.
N.W. Greenland	82° 7′	−38·3°	−39·8°	−35·1°	−26·0°	−10·4°	0·3°
Hammerfest	70°40′	− 5·2	− 4·7	− 3·6	0·0	3·4	7·9
Stockholm	59°20′	− 3·0	− 3·5	− 1·7	3·2	8·4	14·1
Prague	50° 5′	− 1·6	− 0·1	3·1	8·4	13·4	17·2
Naples	40°52′	8·4	9·4	10·8	14·1	17·9	21·5
Cairo	30° 5′	12·4	14·2	16·9	20·8	24·4	27·3
Timbuctu	16°49′	21·8	23·8	28·1	32·5	35·0	34·2
Congo (inland)	0°19′	25·0	25·6	26·0	25·6	25·0	24·5

Place.	Latitude.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Whole Year.
N.W. Greenland	82° 7′	3·0°	0·8°	− 9·0°	−22·2°	−30·0°	−32·3°	−19·9°
Hammerfest	70°40′	11·8	10·8	6·9	1·6	− 2·0	− 3·8	1·9
Stockholm	59°20′	16·6	15·3	11·5	6·2	1·5	− 2·0	5·6
Prague	50° 5′	18·8	18·2	14·6	9·2	3·1	− 0·5	8·6
Naples	40°52′	24·3	24·4	21·8	17·2	12·3	9·4	16·0
Cairo	30° 5′	28·5	27·7	25·3	23·2	18·1	14·4	21·1
Timbuctu	16°49′	32·7	31·1	31·8	31·0	26·8	21·4	29·2
Congo (inland)	0°19′	24·3	24·2	24·0	24·3	27·4	25·0	24·8

1. The equatorial type of climate is characterized by a remarkably small annual variation in mean temperature. Incidental maxima and minima are brought about by other climatic factors, for instance, the rain periods.

2. The second type of climate is the tropical climate; here there is only one maximum and minimum temperature after the summer and winter solstices. The yearly variation of

temperature is still small, and it is markedly influenced by the rainy periods. In the middle of a continent the annual variation is naturally bigger; it reaches 13° C. in Africa, and 18·8° C. in Australia. On the Indian coast, however, the variation is no greater than 5·6° C.

3. In the temperate zones there are marked variations in the temperature throughout the year, so that it is possible to distinguish four seasons, which are particularly marked in the middle regions of this zone. Where the temperate zone borders on the tropics it is difficult to distinguish any definite spring-time, for the increase in insolation is so gradual; and in the sub–Arctic zone the insolation increases so rapidly that there is scarcely any transition time between winter and summer.

4. In the polar climate there is a very marked winter period, owing to the long polar night. The highest temperature occurs in July, and the yearly variation of temperature is very wide, reaching (in Werchojanak) as much as 65·9° C.

Beside these broadly outlined types of climate, a continental and maritime climate can be distinguished. The continental climate is characterized by a greater yearly and daily variation in temperature than a maritime climate upon the same latitude. Another character which distinguishes a land from a sea climate is that in the latter there is a marked lagging of the maxima and minima behind the corresponding extremes of insolation. In a land climate the annual maximum of temperature may follow 25 days after the summer solstice; in a sea climate it may not follow until after one and a half to two months.

The foregoing has referred to temperature differences at sea-level. Now the isotherms on meteorological temperature maps connect together places with the same temperature, after the observed temperatures have been reduced to their equivalent values at sea-level (for the details of this principle see Hann, 1915), on the assumption that the temperature falls 0·5° C. for every 100 metres above sea-level. In a continental climate, therefore, the actual temperature may be many degrees lower than the values indicated by the isotherms. In plant geography, isotherms are only useful in that they give an idea of the gross zonal differences of temperature.

With increasing altitude above sea-level the mean temperature falls about 0·5° per 100 metres, or, according to Schröter, 1° C. for every 180 metres. Upon a sufficiently high mountain on the Equator, therefore, there should be an

Arctic temperature climate; and the regional distribution of the vegetation on high mountains does correspond (allowing for differences due to the different light climate) to the distribution of vegetation over the surface of the earth.

The daily and yearly course of temperature in mountains exhibits certain peculiarities; these are conditioned partly by the thinner layer of air, and the consequent access and radiation of heat, and partly by the horizontal extent and form of the mountain mass. On a high plateau the amplitude of the daily and yearly variations in temperature is greater than on an isolated mountain of the same height. Since the decrease of temperature with height is more gradual in winter than in summer, winter in the Alps is relatively mild; a result approximating to the annual course of temperature in a maritime region, a damping of the extremes of temperature, and a lag of the maxima and minima behind the corresponding values in the lowlands. This parallel is interesting in connection with the parallels often drawn between the floras of mountains and sea coasts.

The yearly minimum in the desert laboratory at Tucson is fully $6°-7°$ lower than that on a neighbouring mountain 820 metres high (McDougall, 1921). The significance of these comparisons of temperature for the distribution of vegetation has been discussed by F. Shreve (1915).

The temperature climate in mountainous regions is very clearly reflected by the course of the tree line. Many investigators have established the fact that the altitude of the forest and the tree line increases with the size of the mountain massif on which the trees are growing. The tree line in the central massif of Switzerland lies 700 to 800 metres higher than the tree line in the outer chains (Schröter, 1923). As the tree line rises in height, so also do the snow line and the isotherms (Figs. 35 and 40).

The area between the tropics is greater than that of the rest of the earth's surface; and it is an extremely important fact in the discussion of the distribution of heat over the earth, that the greater part of the tropics is covered by warm oceans. Fifty per cent of the ocean's surface has a temperature of over $21°$ C., and only 16 per cent a temperature less than $4·5°$ C. This enormous reservoir of stored solar energy moderates to a great extent the cold winter of the temperate and sub-polar zones. Through the influence of ocean currents and ocean winds the January temperature of the Norwegian coast is

increased to the same level as that of North Italy and the
Caspian Sea. The northern limit of the beech, which reaches
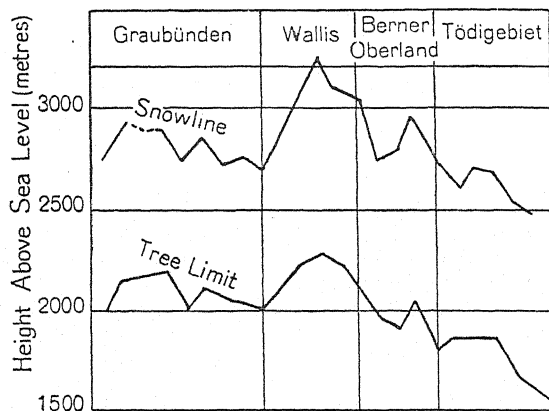
FIG. 40.—Section across Switzerland, showing snow line and tree level.
(Schröter, 1923.)

a latitude of 60° 10′ in Norway, only reaches to 55° 30′ in
Central Sweden, and at Königsberg to 54° 30′. In the same
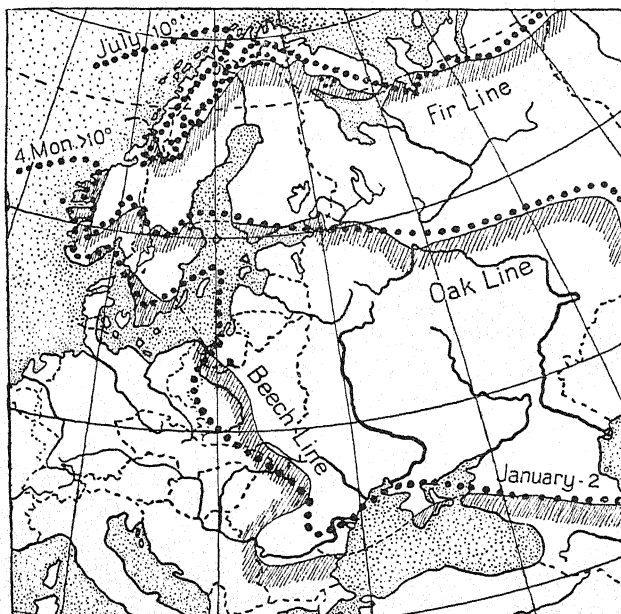
FIG. 41.—The northern limits of Fir, Oak, and Beech, compared with certain
meteorological data. (Walter, 1927.)

way the oak reaches latitudes of 60° 30′ in Norway, but in
Russia it scarcely reaches a latitude of 60° (Fig. 41).

6. Summary of the Influence of Temperature on Vegetation

In the estimation of the action of temperature on the zonal and regional distribution of vegetation, the interference of other factors cannot be overlooked. The temperature factor never operates alone, but in conjunction with the water factor, and often with light. In the foregoing pages two methods of investigation have been described:

1. The correlation method. It is the object of this method to establish correlations between the meteorological data on temperature and the limits of vegetation; critical work has established such correlations. But correlations give no indication of any causal relationship.

2. The second method employs the technique of physiological ecology. The first essential is an exact study of the temperature relationships of the fundamental life-processes. In relating these to natural conditions either of two methods is open. The first is the ecological field study, in which genotypically similar plants are cultivated under different temperature conditions (see Clements and Goldsmith, 1924), and the other factors are kept as constant as possible. This will give an idea of the range within which the plant will flourish.

Against the application of this method lie almost insuperable difficulties. In the transplantations of Bonnier and McDougall, many other factors beside temperature are changed. It would be much more satisfactory to grow the plants in a series of greenhouses in which different temperatures can be maintained.

The second physiological method necessitates the determination in the laboratory of the temperature curves of growth, respiration and assimilation, under conditions as natural as possible. From these determinations conclusions such as the following can be drawn:

The optimal conditions for the accumulation of carbohydrate in sun plants require a day temperature of $10°-30°$ C., depending upon the species and the conditions under which they have previously lived; together with a low night temperature. The significance of the night temperature decreases toward the poles, on account of the longer daily assimilation period. The climate of maritime regions, which are characterized by a high night temperature, becomes more favourable toward the poles.

Owing to their low assimilation optimum, extreme shade plants have their maximum distribution in colder zones. This has been demonstrated for the algal vegetation of the oceans. In sub-Arctic forests, too, in which the day temperature seldom rises above $15°$ C. there is a shade flora rich in comparison with that of sub-tropical forests. Even when the water supply is satisfactory, high day temperatures are detrimental to assimilation, unless the carbon dioxide concentration is also high. As regards their effect upon the carbohydrate balance, supra-
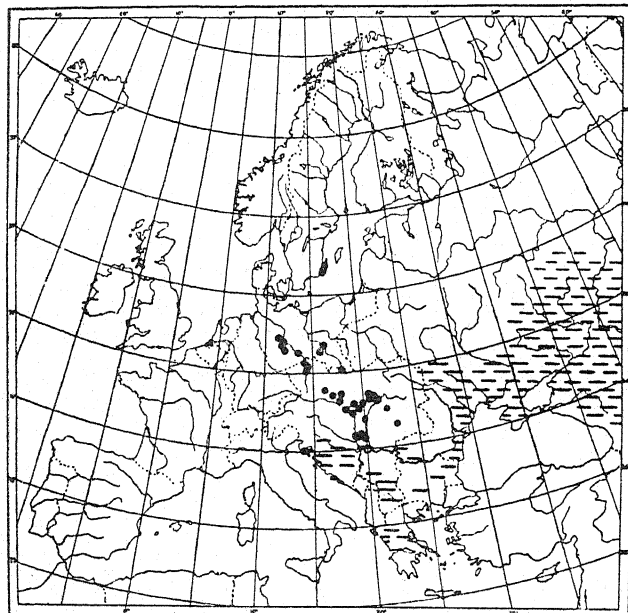
Fig. 42.—The distribution of *Ranunculus Illyricus* in Europe. The black dots represent the western outposts, and the shaded areas represent the main areas of distribution. (Sterner, 1922.)

optimal day temperatures are compensated by low night temperatures. Vahl has attempted to express this in his formula (p. 93).

The effects of climate on the fundamental processes in plants may be summarized as follows:

1. Photosynthesis is determined principally by the climate of midsummer and autumn. This is particularly true for plants with a long assimilation period. Agriculturists recognize that beets give higher yields after a warm, clear, late summer. A cool and rainy spring can be compensated by a warm autumn.

In the Mediterranean zone the assimilation period extends some way into the winter. This is a matter of some importance, for the summer is so dry that very little carbohydrate is formed.

2. Growth is principally determined by the climate of spring. Low temperatures inhibit the development of the vegetation, especially that of spring plants and annuals. A maritime climate, then, with a late and cool spring, is unsuitable for the development of plants which have a rapid life cycle.
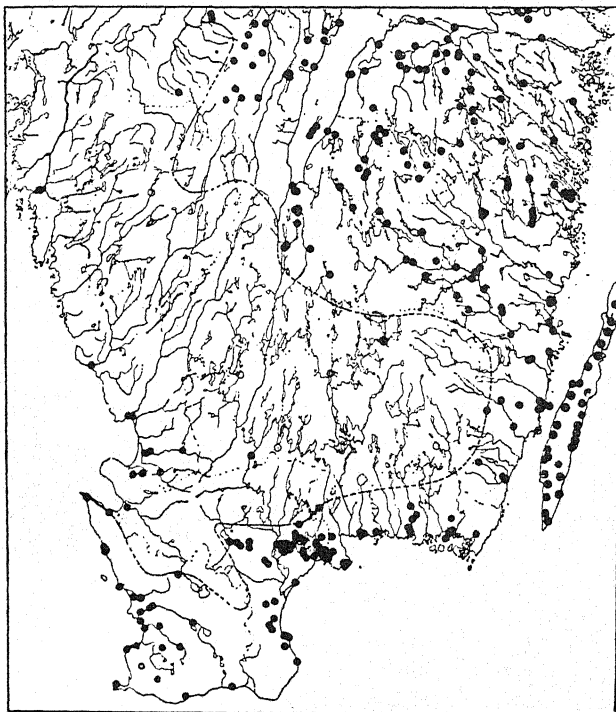
FIG. 43.—The distribution of *Herniaria glabra* in South Sweden (the "Continental type"). (Segerstad, 1924.)

3. The ripening of fruits is promoted by a high temperature in late summer and autumn.

4. The over-wintering of seeds, buds, and certain reproductive organs is often increased by frost.

The temperature climate, therefore, falls into four ecological periods, more or less corresponding to the seasons. The first is the *growth period* (spring), when increase of temperature has a consistently favourable effect, at any rate up to temperatures of 30° C.

The second period is the *assimilation* period (summer–autumn), when high (but not too high) day temperatures and low night temperatures are most favourable.

The third period, the period of *fruit formation*, occurs in the autumn; at this time the most favourable climate is one with moderate day and night temperatures. Lastly, in the *after-ripening* period (winter), low temperatures, so long as they are not too low, are advantageous.
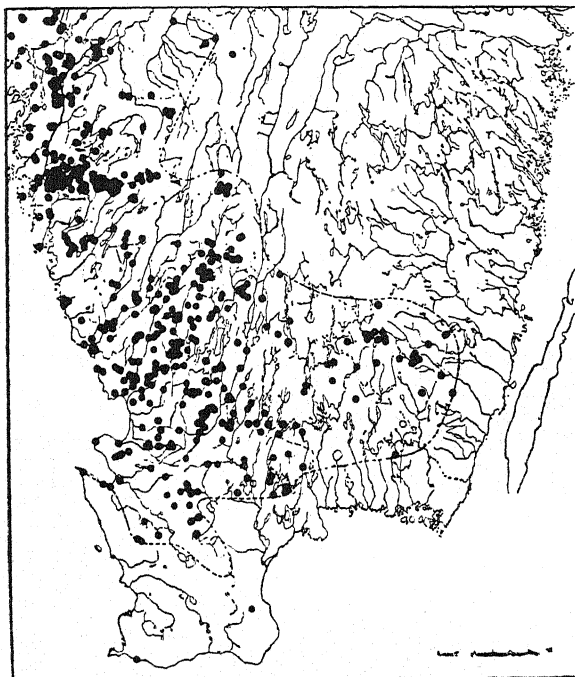
FIG. 44.—The distribution of *Narthecium ossifraga* in South Sweden (the "Atlantic type"). (Segerstad, 1924.)

These conditions apply only to those regions with a marked annual periodicity of climate, especially the temperate zone. Within this zone there are a number of vegetation types, the length of whose vegetative period determines their distribution. Further divergences in distribution depend upon the amounts of warmth in the different seasons. A continental vegetation type is determined by the growth period and the assimilation period; while a maritime vegetation type depends upon the second period alone.

In Europe there is a gradual transition from east to west, from the continental climate of Asia to the maritime climate

of Western Europe.   In the east is a "continental type" of flora (Sarmatic type), and in the west a "maritime type" (the Atlantic flora).   Sterner (1922) and Av Segerstad (1924) have published some interesting work upon the extent of these two floral types (Figs. 42, 43 and 44).   Only by experimental methods can it be discovered to what degree the distribution depends upon temperature, and to what degree upon water and soil.

CHAPTER IV

THE WATER FACTOR

THE third of the dominating factors which determine plant distribution, after temperature and light, is the water factor, and of these three the water factor has the most striking effect upon vegetation. The distribution of soil moisture and rainfall bring about, more than any other factor, the manifold types of vegetation.

From the purely physical aspect, the water factor can be divided into three constituent parts: rainfall, soil moisture, and humidity of the air. These vary to some extent independently, and only when considered altogether do they determine the action of water as an ecological factor. The issue depends upon the total water balance, that is, the relationship between the amount of water which the plant takes up, and the amount it loses by transpiration. Under normal conditions the ratio, water uptake/transpiration, cannot sink for long below unity. The power of resistance against wilting, however, varies very much; and here lies the real difference between mesophytes and xerophytes. A succulent plant can stand a great deal of wilting without losing its life; mosses and lichens are still more resistant; shade plants in the temperate zones, on the contrary, are usually very sensitive to desiccation. Higher plants can regulate their water loss within wide limits, by means of stomatal movement; and the "incipient drying" described by Livingston, whereby the suction pressure of a cell increases as the cell shrinks, is to some extent a regulation against water loss.

The external conditions which affect transpiration are relative humidity of the air, temperature, and wind. Their action is purely physical; but on account of the regulatory processes mentioned above, which depend upon the fluctuating water balance, the transpiration rate is not determined by these alone. Other factors, too, such as light, affect the stomatal aperture, and therefore interfere in transpiration.

As with light and temperature, so with the water factor, it is insufficient to assess the effect from yearly integrations of the amount, for the distribution of rainfall throughout the year is in itself a very important factor. Continuous heavy rain has an action quite different from that of frequent showers, even when the total rainfall is the same in both instances.

The physical structure of the soil determines how much of the rain comes within reach of the roots, and is held there, and how much flows through the soil or runs off its surface. Temperature and wind determine how much water is lost by evaporation; and in an open formation these factors play a considerable part.

1. Water in the Soil

The water factor is peculiar in that it is at once a climatic factor and a soil factor; and it will be advisable to begin our discussion with a consideration of the water-storage capacity of the soil. The water stored in the soil may be classified into three groups: hygroscopic water, capillary water, and gravitational water (Ramann, 1911; Russell, 1923.)[1] Hygroscopicity may be defined as the power of solids to adsorb water upon their surface; the larger the relative surface, the larger is the hygroscopicity. Now the soil, since it consists of minute particles of minerals and humus in the colloidal state, has a very great "internal" surface, so that its adsorptive capacity for water vapour can be measured with a balance. The following method was used by Mitscherlich (1920):

Completely dry soil was put in a vacuum over 10 per cent sulphuric acid, and the uptake of water was followed by weighing. Subsequently Mitscherlich has employed an oil-benzole mixture. The uptake of benzole was measured and from this result the extent of the internal surface was calculated. The real significance of Mitscherlich's method has not yet been fully established. The calculations of the internal surface of soils

[1] Gradmann (1928) has recently introduced the following classification: (1) "pendular state"—no continuous capillary water, but continuous air spaces in the soil; (2) "funicular state"—continuous capillary water system, and co-existent continuous air system; (3) "replete state"—continuous capillary water system, but no continuous air system in the soil. State No. 2 is characteristic for mesophytes, and State No. 3 for hygrophytes. State No. 1 distinguishes very dry soils which will only support desert plants for a limited time.

I

from his values are for the most part much higher than the results calculated by other workers (Ehrenberg, 1918).

According to Mitscherlich, a thick clay soil has an internal surface of 9,667·7 square metres per gram of soil. Odén, on the other hand, in a red Atlantic deep sea clay, finds an inner surface of only 1·7 square metres, and the results of other investigators are of this order of magnitude. In spite of its apparent unreliability for absolute measurements, Mitscherlich's method is a notable contribution to the determination of the relative absorptive capacities of soils. A knowledge of the distribution of water in soils is important not only for the study of water storage capacity, but also for the study of the uptake of salts. Water, as such, held hygroscopically in the soil, has a very subordinate influence upon plant life. (*See* Mitscherlich, 1920; and Bachmann, 1922.) A layer of adsorbed water 10^{-5} cm. thick, develops a capillary force of from 14 to 15 atmospheres. The water of greatest importance is that held by capillarity, and the amount so held depends upon the size of the particles and the state of subdivision of the soil. With a decrease in the size of the particles, not only is there an increase in the height to which the water is drawn, but the amount of water held by the soil also increases. A finely divided soil, therefore, holds a greater amount of water drawn from below than a soil with large particles, like sand. The height to which water rises in different soils has been determined by Tulaikow (1907), Atterberg (1908) and Mitscherlich (1920). The highest values observed were between 1·35 and 1·5 metres.

Water held by capillary attraction is not influenced by gravity. It has been customary to measure the amount of water held in this way by allowing saturated soil to stand in a cylinder with a perforated base, until the "free water" has flowed away. The amount of water still retained by the soil is the water held by capillarity together with that adsorbed on the soil particles. But since the capillarity of a soil depends upon its temporary condition, it is very difficult to determine by experiment the water capacity of natural soil. In the same soil the water capacity may vary from 15 to 40 per cent, according to the degree of division of the soil particles (Ramann, 1911; Russell, 1921). Wahnschaffe and Schucht (1914) have described a method for the determination of water capacity of soils under natural conditions in the field. The water held by capillarity is of great significance for vegetation,

since it provides a reservoir from which the plant can draw in times of low rainfall.

The gravitational water is that surplus of water which, after rain, gradually sinks downward, under the influence of gravity. This water is only loosely held by the soil, rather in the manner of the water in a fully imbibed sponge. When the rain showers follow one another sufficiently often, this water, too, forms an integral part of the soil moisture, and can be of importance in soils like sand, which have a low water capacity. In heavy soils, on the other hand, this water can be definitely harmful, since it inhibits aeration. A crumbling spongy soil has this advantage, that it facilitates the drainage, and the breaking up of a soil in this way does not lessen the amount of water held by capillarity, and therefore the water capacity of the soil remains the same. Breaking up the ground is important, too, for it facilitates the entry of water into the soil.

In arid places very small differences in the water capacity of the soil can influence the vegetation. Consider, for instance, two soils, one having a water capacity of 5 per cent, and the other one of 25 per cent. A rainfall of 30 millimetres might permeate 60 cm. into the former soil and only 12 cm. into the latter. It is evident that in the coarse soil deep-rooted plants will be in the majority, while in the soil of finer texture shallow-rooted plants will predominate. (This assumes, of course, that the level of the water table is so low that the capillary rise from below does not come into question.) Even in humid places, differences in water capacity can be significant, since the aeration may be affected. Numerous examples of big differences in water content in closely adjacent soils have been given by Kraus in his memoir (1911).

The extraordinary significance of water storage capacity of soils for plant growth has assured that these relationships should receive the full attention of ecologists. It is evident, however, that purely physical investigations do not lead very far, but must always be coupled with investigations of the actual capacity of the plant to take up water from the soil. Very little significance can be attached, for instance, to values of the absolute water content of a soil, for the last 10 per cent of water in a humus soil is held with much greater force than the last 10 per cent in a sandy soil (Shull, 1916). American workers have sought to express this difference by determining the "wilting point"; this work will be discussed subsequently.

2. The Water Content of the Soil and Growth

The influence of the water factor alone upon growth, without the interference of other factors, takes the form of a decrement curve, of the same general shape as the assimilation curves described on page 29; this has frequently been found by Mitscherlich (1927) and Gehrmann (1927). In pot-culture experiments, when the water content of the soil is raised, the yield increases too, at first rapidly, then more slowly.

In Nature the water content cannot be raised at will, without involving the interference of other factors, especially aeration. The more water there is in the soil, the less "pore space" is there, and the less aeration. The curve of water content against yield, therefore, exhibits an optimum, and is composed of two curves, a rising "water curve," and a falling "aeration curve." The position of the optimum differs widely for different plants, for their susceptibility to aeration varies greatly. (Table XX.) (Mitscherlich, 1920.)

Table XX

| Plant: Relative Yield of: | Water Content in Percentage of Water Capacity. | | | | |
	20	40	60	80	100
Summer rye	30·7	71·4	92·8	77·6	19·7
Peas	14·1	50·3	87·4	100·0	9·3
Horse-beans	16·0	48·4	63·9	100·0	33·8
Potatoes	15·8	48·3	89·0	100·0	62·5

The soil was a diluvial sand with 4 per cent humus and 2 per cent chalk. Between water contents of 60 per cent to 80 per cent, a change in the water content had very little effect, water being here in maximum. Fittbogen, using oats, found that the yield at 40 to 80 per cent water content was about the same. At a water content of 20 per cent, only half this amount was harvested, and at 10 per cent, only one-eighth. Shive (1910) obtained optimal growth of corn at a water content of 60 per cent, in sand cultures. In soils relatively poor in water, therefore, such as occur in the arid regions of the earth, water plays a greater part as a limiting factor in growth than in soils of high water content. In arid regions water is the deciding factor in plant distribution (Clements, 1916).

When the water factor is supraoptimal, consideration must be taken of the "aeration curve." The end part of the curve, for a great many species, falls very rapidly (Fig. 45). This rapid fall of the curve would account for the very sharp transition between bog vegetation and mesophytic vegetation, especially in deciduous woods. Bog plants never trespass outside the limits of the bog, and the mesophilous shade plants stop short at the edge where the moisture becomes excessive. As the soil dries out in the course of the summer, the edge of the mesophilous vegetation moves forward. At
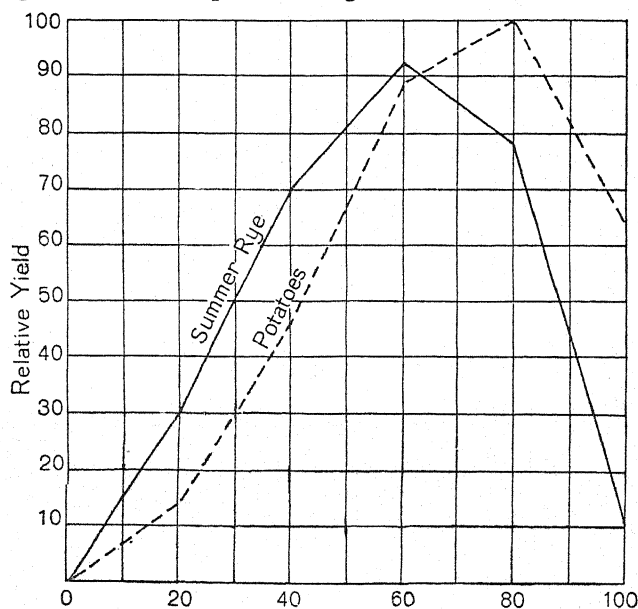
FIG. 45.—Yield in its relation to the water content of the soil.

the edge of a bog in Hallands-Väderö grows *Dryopteris thelypteris*, which spreads centripetally as the bog dries out. In dry years *Oenanthe aquatica* thrives in dry boggy soils, while in wet years it disappears (Plate IV).

Feilberg has given examples of the action of water as it becomes a minimum factor (1890). (*See* Warming, 1915–18; Waff, 1923; Jeffreys, 1917; Weber, 1913). In the sandy plains of Skagen in Jutland the height of the water table, and the differences it causes in the water content of the upper layers of the soil, are reflected in the vegetation. In summer, when the water table is 3 inches deep, there is a Juncus vegetation, and a "moor" formation. When the level has sunk to

6 inches, mosses and Cyperaceae are still present, but grasses begin to appear; and at a depth of 9 inches, grasses are dominant.   When the depth reaches 12 inches a normal grass meadow predominates, and with a water-level as low as 15 inches, cereals can grow.   At 18 to 24 inches, cereals can only grow in a cold, wet summer.   When the depth of the water reaches 30 to 40 inches, the ground is useless for corn, and only typical xerophytes remain.

The growth of root and shoot are not influenced equally by the water factor (Seelhorst, 1900).   (*See also* Weaver, 1919, 1920.)   When the water content of the soil is low, the root system is highly developed, while the aerial part remains small.   In the presence of a superabundance of water the root system is poor, while the green parts grow luxuriantly. Little is known of the plasticity of species, but it is evident that the power of a plant to regulate the size of its absorptive system according to the "ecological intensity" of the water factor, must be of great importance in the struggle for existence.

Weaver has made interesting observations upon the plasticity of adaptation of several prairie plants (1919) (Fig. 46).   The development of the root system of ten polydemic species was followed in at least two different sorts of habitats.   Seven of these showed a striking adaptation of their roots to the available water, while two or three species, *Allionia linearis*, *Abronia fragrans*, and *Koeleria*, exhibited very little plasticity of the root system.

FIG. 46.—The root system of a prairie plant, *Kuhnia glutinosa*. The roots branch most richly in the damper layers of soil. The root system is 17 feet deep.   (Weaver, 1919.)

Certain other morphological changes are influenced by the water factor.   It is known, for instance, that cereals, especially corn and rye, ripen with difficulty in a very damp climate. Even the chemical composition of corn grains is profoundly influenced by variations in the available water (Shutt, 1910; Bailey, 1913).

PLATE IV

Alder swamp, (*a*) dried out in summer, with *Dryopteris thelypteris* around the bases of the alders; (*b*) the same swamp in a wet summer, with a rich ground vegetation of *Oenanthe aquatica*, and on the right, *Iris pseudacoris*.

As a rule, plants need more water in the vegetative than in the fruiting period, a fact which is of importance in gardening, and which naturally plays a part in Nature, where a constant humidity seldom prevails throughout the year. Schimper (1898) has pointed out how, in many tropical regions, the flowering period falls in the dry season, or at any rate at a time of low rainfall. Even in temperate zones the flowering time of many plants falls in that part of the summer which has the lowest rainfall.

The importance of this correlation between reproduction and water is illustrated by the ecology of steppes and prairies. Owing to the winter rains, the soil is damp in spring, and the steppe plants can rapidly develop their vegetative system. In the course of the season, however, the soil dries up, and vegetative extension becomes impossible. The plants flower rapidly and complete their life cycle.

Similar though less extreme conditions of life are to be found in Scandinavia and Britain, on rocky soils or on sand dunes, where the water capacity is low. The only plants which succeed in such habitats are those which flower rapidly in response to the relatively dry midsummer; plants such as species of *Bromus, Aira precox, Anthoxanthum odoratum,* and so on. In damp places these plants remain until late summer in the vegetative condition, and it is well known that many meadow grasses growing in woods flower only very late, or do not come to flower at all; though to what extent light is responsible for this is not known. Among algæ, too, and fungi, decreasing moisture is often the stimulus for the formation of reproductive organs (Kessler, 1914).

For the critical evaluation of these and similar observations it is naturally absolutely essential to gain as complete an understanding as possible of the water-climate of a habitat. For this purpose the physical structure of the soil must be taken into account, and the structure and porosity of the bedrock beneath. Information will be needed as to the amount and distribution in time of the rainfall, and the extent of evaporation from the soil surface. This latter will depend upon the colour and roughness of the soil surface; as a rule, a bare soil loses in unit time only 1/2 to 1/3 as much water as a similar soil covered with vegetation (*see* Mitscherlich and Hartmann, 1928). Rainy periods alternate with periods of drought, and the soil water content changes perpetually, more

so in a sandy soil, of low water capacity, than in a soil of high water capacity, like a clay (Russell, 1927).

The depth to which rain-water penetrates in the soil depends greatly upon the soil structure, and this structure determines the height to which water will rise by capillary attraction, and the speed of this transport. The water content is continually reduced in the immediate vicinity of the roots, and the rate at which this deficit is made up from the adjacent soil is often of importance to the plant. On moors (Odén, 1919) the rate of water movement is very slow, and this has been suggested as one of the causes of xeromorphy among moorland plants. In handbooks of soil science (Ramann: *Evolution and Classification of Soils*, Eng. trans., 1928) these physical relationships are fully discussed, so that it has not been thought necessary to do more than refer to these phenomena here.

3. The Water Factor and Transpiration

As a soil loses more and more water by evaporation a point is finally reached where growth stops, and the life of the plant is threatened. At this absolute ecological minimum of the water factor, when the loss of water through transpiration exceeds the uptake, the plant wilts: the suction pressure of the root has become smaller than that of the soil.[1] The position of the wilting-point changes with the intensity of transpiration, and accordingly with the humidity of the air. (*See* Caldwell, 1913; Shive and Livingston, 1914; Blackman, V. H., 1914.) The wilting-point, then, must be determined at some definite known humidity, and in addition the stomatal aperture must be known.

A great many attempts have been made to measure the water-retaining power ("suction pressure") of the soil. The method adopted by Shull (1916) was to measure the imbibition by seeds in the soil. He found that in a heavy clay soil, from 20 to 80 per cent of the water is very loosely held, below which the power with which the remaining water is held rises rapidly, and reaches 100 atmospheres at a water content of 5 per cent; most of this water being adsorbed on the soil particles. There is no evidence of water adsorption on sand until the water content is much lower than 5 per cent.

[1] The "suction pressure" of the soil will be used here as an abbreviation of the "water retaining power" of the soil. (*See also* Shull, *Bot. Gaz.*, LXXXIX, 1930, p. 583.)

Other investigators have, without any striking success, tried to use "artificial roots," osmometers or clay cylinders filled with an osmotically active solution, and which are put into the soil (Livingston, 1915; Pulling, 1917). Bachmann (1927) and others have compared the lowering of the vapour pressure over the soil with that over a free water surface. A simple and apparently reliable method is that of the solution hygrometer. The method depends upon the lowering of the vapour pressure, but the pressure is not measured with a manometer, but through the uptake or loss of water from a filter paper soaked in sugar or salt solution (Hansen, 1926; Gradmann, 1928).

Recent work has confirmed the conclusions of Shull in establishing that the relation between suction pressure of the soil and water content followed an exponential curve. It is only the last few per cent of the water which is held with particular force in the soil (Fig. 47). The behaviour of different soils varies widely, especially as water movement in the soil and other factors come into play.

FIG. 47.—The abscissae represent the water content of the soil in percentages of the total capacity. The ordinates represent the relative lowering of the vapour pressure. (After Bachmann, 1927.)

I   Sand
II   Peat mull
III   Sawdust
IV   Garden Soil

Livingston has evolved a valuable method for investigating the soil suction pressure ecologically, namely, his so-called "soil point." A cone of porous clay, glazed above and below, is weighed, and pushed into the soil. After a certain time it is removed, cleaned, and weighed again. By the aid of this method Livingston found that 3·64 gm. of water were removed from a saturated soil in half an hour, while from a soil at the wilting-point of wheat only 0·09 gm. was removed in two hours.

From the standpoint of physiology, wilting is no sudden

condition of the plant, but denotes a gradual transition from a condition of positive to a condition of negative water economy. Turgescent root cells, completely saturated with water, have a suction pressure of zero, and will therefore absorb no water. Only when the cell wall has lost its turgidity is water taken up from the surrounding medium; a process which continues until turgor is re-established. In a completely contracted cell, the suction pressure is equal to the osmotic pressure; this condition is only reached upon complete wilting. It is scarcely surprising that permanent wilting occurs somewhat earlier, since, according to Shull, the opposing pressure in the soil at wilting-point is about 4 atmospheres, while the osmotic pressure of the root is usually somewhat higher. In certain mesophytes Bachmann (1927) found wilting to begin when the soil suction pressure lay between 1 and 2 atmospheres.

Plants which are able to endure severe wilting without suffering any harm are naturally able to develop a very high suction pressure. From this standpoint should be regarded the succulents, where a low osmotic pressure is combined with a marked resistance to wilting. On the other hand, shade plants, which are very susceptible to wilting, have little "use" for their osmotic pressure, since they are seriously harmed directly the suction pressure begins to rise.

An essential part in the plant's economy is played by the movement of water through the plant. The aerial parts give up water continuously by transpiration, and make good the loss by conduction from the roots. Thereupon the turgor falls in the roots, and these absorb water from the soil. The water balance does not depend only upon the absolute suction pressure, but upon the speed of conduction through the plant, and the speed of movement through the soil. Livingston and Hawkins (1915) have attempted to determine the relation between transpiration and movement of water through the soil at different times of the day. The suction pressure of the roots was measured indirectly, by sinking in the earth a porous clay cylinder full of water, closed at the top with a rubber cork through which a measuring tube passed. The fall of the water-level in the measuring tube gave the speed with which water was lost into the soil, and this speed in its turn depends upon the state of saturation of the soil. It was found that early in the morning transpiration was much more rapid than the absorption of water from the clay vessel. Therefore at midday there is a marked deficit in the soil. In the afternoon

this deficit is rapidly reduced, but not until the next morning is the balance again restored. This experiment emphasizes the importance of water conduction in the soil as a factor in the plant's economy.

Briggs and Shantz (1916) have carried out some very interesting work upon the daily march of transpiration. They used an automatic transpiration balance which registered directly the hourly transpiration from plants growing in pots weighing 115 kilograms, standing in the open. Throughout the experiments the principal climatic conditions were auto-
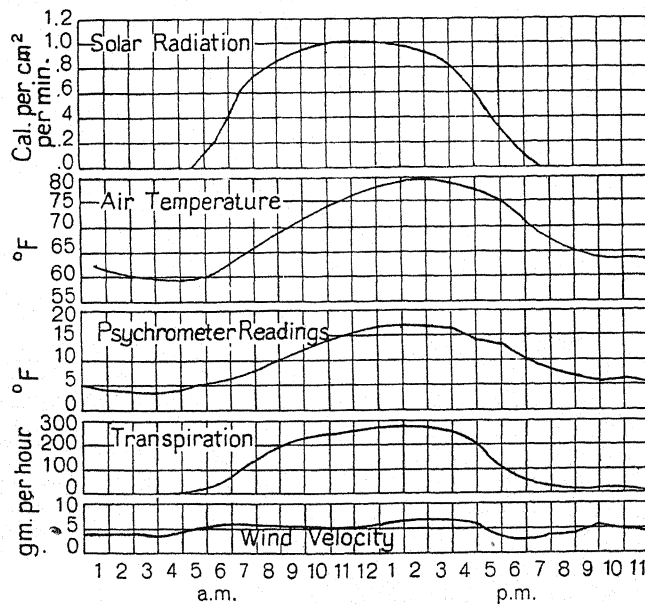
Fig. 48.—Transpiration throughout the day for oats, together with the principal factors affecting it. (Briggs and Shantz, 1916.)

matically registered, viz. total radiant energy (by means of a blackened thermometer in the sun, and a polished thermometer in the shade), air temperature, wind, and the evaporation from a free water surface.

In Figure 48 are given the results obtained with oats, on a clear day. Transpiration is very low at night. It rises quickly at sunrise, and reaches a maximum about midday, after which it sinks again toward the evening. The correlation coefficient of transpiration and radiant energy is 0·66— 0·75. Parallel with the radiant energy curves are curves of

air temperature and humidity, though the significance of this parallelism is uncertain. Wind has the least effective influence.

The work of Briggs and Shantz was carried out under "ideal" conditions, especially as regards the water content of the soil. In nature, however, the moisture content varies continuously, and the work of Livingston and Hawkins (and of Maximov, 1923, and Iljin, 1922, *b*) shows that at the time of greatest transpiration there is a temporary water deficit in the soil. Under these conditions stomatal regulation comes into play, and the normal course of transpiration is markedly altered. Stomatal movements are also of great significance in the carbon dioxide economy of the plant.

Most plants shut their stomata in decreasing light, sometimes as much as an hour before sunset. Bachmann (1922) found that the minimal stomatal size of some plants was reached at 6 p.m. In repeated experiments the writer has found that even in clear weather the stomata of the potato plant are shut between 4 and 5 p.m.; and Weber has arrived at similar results with *Aesculus* (1923). In spruce and pines, according to Stålfelt (1924), the stomata close on rainy days between 5 and 7 o'clock in the evening.

It is principally light, therefore, which determines the periodic movements of stomata during the day; though there are plants whose stomata remain open in complete darkness. This is the case with *Solanum Lycopersicum*, in which plant the writer has found stomata still open at 9–10 p.m. in October. It is doubtful, indeed, whether they ever shut at all. These observations, it should be stated, were made upon greenhouse plants.

The stomata of the majority of plants, however, belong to the light sensitive type, and of the behaviour of these, much remains to be discovered. For instance, it is not known whether the opening and closing always takes place at the same light intensity. Benecke's statement (1924) "that the stomata close at every passing shade, even a shower of rain," seems to the writer to be questionable. The writer has observed that in rainy weather stomata remain open almost as long as in clear weather; this would seem to follow, too, from the results of Weber and Stålfelt. Since stomatal movement is regulated by changes of turgor in the guard cells, and since these changes are influenced by light, by moisture conditions, by dissociated salts (Iljin, 1922), and by the whole water balance of the plant (Stålfelt, 1927), it can scarcely be sup-

posed that the movement will exhibit any simple relationship
to the prevailing light intensity.   In recent years Stålfelt has
studied the mechanism of stomatal movement more closely
(1927, *b*, 1928).   He has found that the change of stomatal
aperture follows a rhythmic curve, which begins almost
directly on exposure to light, and which seems to bear a
certain quantitative relationship to light intensity.

The behaviour of the stomata under natural conditions
may be considered as the resultant of the interaction of
light, humidity, and stomatal movement.   If light alone
determined the movement, the daily period of opening
would be about 10 hours (Fig. 49).   But on clear and sunny
days a depression in the humidity of the air sets in, and
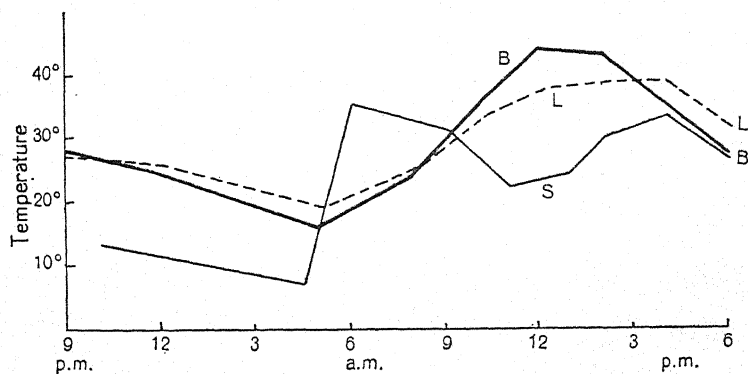
FIG. 49.—Air temperature (° C.), L; leaf temperature, B; and stomatal aperture, S, in course of
the day.   (E. B. Shreve, 1914.)

the transpiration exceeds the uptake of water.   Thus the
"humidity curve" interferes with stomatal aperture, and a
closing of the stomata is observed in the middle of the day.
Under favourable conditions this closure is only partial and
temporary (Fig. 50).   But often, in dry, hot weather, the
stomata close soon after opening, and remain closed until the
next morning.   This has been described by Weber as the
"fair weather" type of stomatal opening; that such a type
exists has been confirmed by the observations of Stålfelt and of
the author.   In the "bad weather" type, which occurs on a
continuously rainy, cloudy day, the stomata open an hour or
two later in the morning, reach their maximum in the fore-
noon, and remain open until the evening.   Naturally these
two types of movement do not cover all the examples found
in nature.   Loftfield (1921) distinguished several types of

mechanism depending upon different combinations of light and humidity. (*See also* Leick, 1927.)

These types of movement occur in sun leaves. In shade leaves the stomata are open much less; in some plants they seem to be constantly shut (Weber, 1923; Lundegårdh, 1924, *a*, p. 97). Since a plant such as *Viola palustris* has its stomata open in deep shade (Lundegårdh, 1921, *b*), it can be
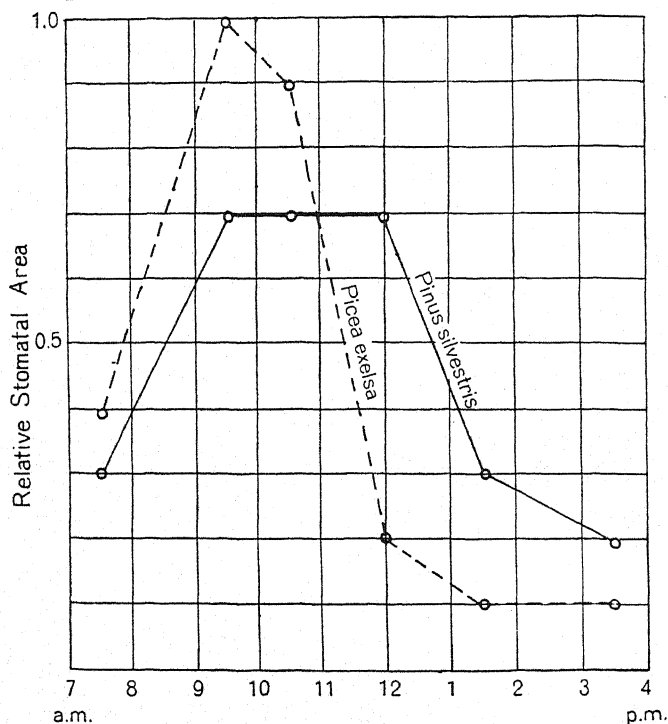
Fig. 50.—Daily course of stomatal aperture. Weather: morning, rain; 8.30 a.m., clear and calm; morning, clear to partly clouded; 2–4 p.m., clouded and rain. (After Stålfelt.)

assumed that the stomata are influenced by much lower light intensities than are those of sun plants. The stomata of *Oxalis acetosella*, on the other hand, in the shade of a wood, remain shut or only partly open, and the author has made similar observations upon other plants. Leick's work has demonstrated that the effect of light upon adaxial and abaxial stomata can vary widely. Such data show that it is impossible to formulate general rules on the subject.

Stomatal movement will influence not only transpiration, but the gas exchange necessary for photosynthesis. Extensive

observations upon the change in transpiration with changing
external conditions have been made by Cribbs (1919; 1921)
and Loftfield (1921). Cribbs has followed the daily march
of transpiration in leaves of *Tilia americana* by Stahl's cobalt
chloride method. He found that the shape of the curve, even
in the same leaf, changes from day to day, depending upon the
relative humidity, the temperature of the air, the light inten-
sity, and the soil temperature. The close correlation between
transpiration and soil temperature is very interesting. The
transpiration in the morning rises more rapidly if the tree is on
a sandy soil than if it is on a clay soil, and on a clay soil the
daily maximum is lower. Further observation revealed what
might have been expected, namely, that the transpiration of
shade leaves of *Tilia*, in a wood, is much less than that of
leaves of the same plant out in the sun.
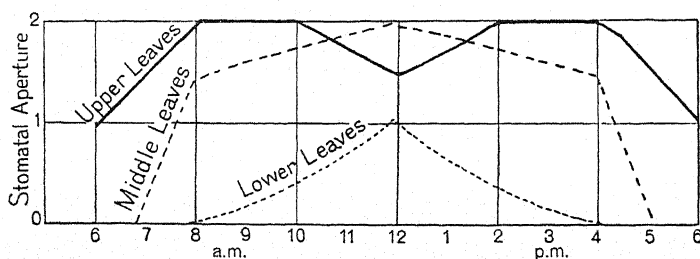
FIG. 51.—The daily course of stomatal movements in potato leaves; somewhat
diagrammatic. (After Lundegårdh, 1924.)

Loftfield followed simultaneously transpiration and
stomatal aperture. His method was to strip the epidermis
with forceps and to plunge it immediately into absolute
alcohol, after which the condition of the stomata was examined
under the microscope. A very close parallelism between
transpiration and stomatal movement was found (Figs. 52, 53).
The correlation was particularly good when the aperture was
small. Naturally at bigger apertures, a slight change in
the dimensions of the stomata made less difference in the
transpiration. This question requires further investigation.
Experiments with perforated metal foil have been carried out
by Sierp and Seybold (1927; 1928) and by Hüber (1928).

With regard to transpiration, the same relationship holds
as was found to hold for photosynthetic exchange, namely, that
the dimensions of a fully open stoma are, as it were, excessive.
It would allow of a more intensive gas exchange than the leaf
can afford (Lundegårdh, 1924, *a*, p. 100). This, together

with the fact that the closing mechanism occupies a certain time, means that the plant is imperfectly protected against emergencies in its water economy, when the transpiration uptake ratio suddenly increases.

It is just at this point that the "incipient drying" described
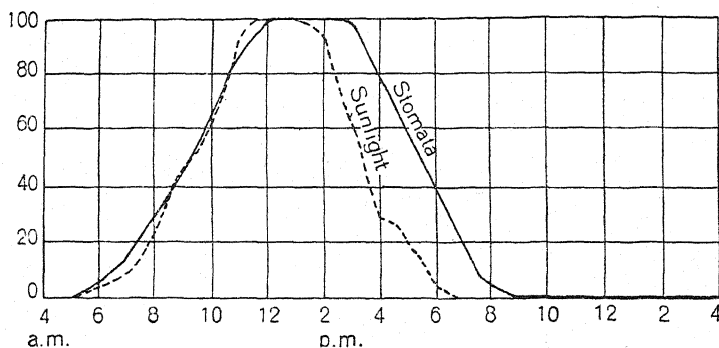
FIG. 52.—The relation between stomatal aperture and sunlight in Alfalfa.   (Loftfield, 1921.)

by Livingston and Brown (1912) sets in.   By "incipient drying" is meant that state in which the osmotic pressure of the leaf cells increases with the water loss, while the vapour pressure and the transpiration automatically sink.   This
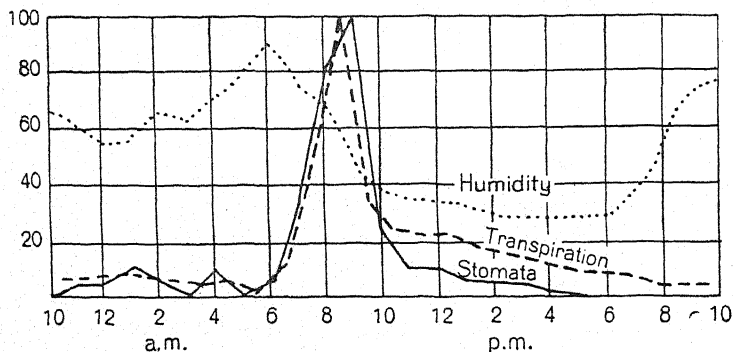
FIG. 53.—The daily course of stomatal aperture and transpiration in a cut shoot of Alfalfa.   (Loftfield.)

decrease in the transpiration before the closure of the stomata has actually been observed by Shreve (1914) and Knight (1917).   Such a process can play a part in the economy of the plant when the plant can withstand partial wilting, as in sun plants, and especially in xerophytes.   "Incipient drying" has also been discussed by Renner (1915) and Benecke-Jost (1924).

4. The Measurement of Transpiration

For transpiration measurements the general principles put forward for the measurement of other ecological factors must be followed. Regular quantitative observations must be taken. Extremes in the water economy are of greater significance than extremes of light or temperature. A single wilting can do irreparable damage to the plant. Even when a plant seems superficially to have withstood wilting, yet, as Iljin has shown (1923), its photosynthesis may be checked, and its respiration may rise, so that the whole balance of nutrition is shifted in an unfavourable direction.

On the other hand, a continued saturation of the air, and a continued turgescence of the leaf cells, exert an unfavourable influence upon the uptake of salts and upon translocation. Costerus (1895) and Faber (1915) have both observed that in a damp tropical forest the removal of starch from the leaves by night is only partially completed. Molisch (1921), who has worked upon this subject, has found that starch disappears from the leaves at night more rapidly if the leaves are strongly transpiring. This may depend upon the concentration of the cell sap rather than upon transpiration itself. In 1914 the writer found that in plasmolysis the starch is actually dissolved, and this discovery has since been confirmed by the observations of Schroeder (1922) and Iljin (1922). Still more recently Ahrns (1924) has found that at the time of wilting the starch disappears, while the sugar and hexose contents increase. In the light of these facts the midday decrease in the turgescence of the leaves is not altogether a disadvantageous phenomenon. It is questionable whether most plants are able to assimilate the whole day long at full intensity, since the cells become choked with assimilates. During the temporary decrease of turgescence the assimilation is held up, owing to the closure of the stomata, and the translocation of the assimilate is accelerated. Detailed work upon this point would be of great interest.

The direct measurement of transpiration by weighing—the only method free from theoretical objections—is not practicable for plants rooted in their natural habitat. The transpiration of cut shoots, unlike their assimilation, is quite different from that of shoots *in situ* (Loftfield, 1921). The potometer, too, is unsuitable for ecological work. There would be wide application for a method whereby the trans-

piration of a leaf could be measured directly after cutting it off, i.e. before the stomatal aperture or the osmotic pressure have had time to change. These conditions are fulfilled to some extent by the cobalt method of Stahl, but the method has other objections, especially as regards the quantitative evaluation of the results. The cobalt method can naturally be employed upon leaves *in situ*; a number of investigators have described improvements in the cobalt method suitable for this purpose (Bakke, 1913; Trelease and Livingston, 1916; Rübel, 1919; Hüber, 1924). Quantitative results can be obtained by this method when the transpiration T is compared with the simultaneous evaporation E from a free water surface. The quotient T/E has been called by Livingston (1906) the "relative transpiration." Stocker (1928; 1929) has recently obtained good measures of transpiration by weighing leaves and twigs on a balance at short intervals of time.

By the use of the cobalt method, or by weighing, the total transpiration is measured. By other methods such as the alcohol infiltration method of Molisch (1912), or the water infiltration method of Neger (1912), or by microscopical examination (Gray and Pierce, 1919; Loftfield, 1921), it can be discovered to what degree stomatal movements influence transpiration.

Generally speaking, transpiration and assimilation are, so far as their physiological action is concerned, influenced in directly opposite ways by stomatal movement.

In most cases it is the water regulation which dominates. Thus the midday closure of the stomata in the "fair weather" type of movement is very inexpedient for assimilation, which, as Thoday has shown (1910; *see also* F. T. McLean, 1920), can be inhibited altogether. On the other hand, the carbon dioxide taken in for photosynthesis is far less in quantity than the water vapour evaporated; and owing to the different rates of diffusion of the two gases, with decrease in stomatal aperture, the rate of transpiration is reduced earlier than that of assimilatory exchange. The various arrangements whereby stomata are sunk and protected against wind enable a greater assimilation per unit loss of water to be carried on. In shade plants the thin cuticle probably admits of intake of carbon dioxide; in many of these plants we know very little of the quantitative effect upon assimilation of a change in the stomatal aperture (p. 128). It is evident, however, that in extreme cases, on dry sand dunes, for instance, plants do not suffer so

much from direct water shortage as from shortage of carbon dioxide: they are starved. The power of xerophytes to form acids in this emergency is perhaps some compensation to them (p. 72).

A certain amount of light is thrown upon these relationships by the determination of the relative "water requirement" of plants, in other words, the amount of water given out per unit amount of dry matter formed. The smaller this coefficient is, the greater has been the plant's success in combining (by morphological or physiological means) the maximum amount of gas exchange with the minimum transpiration. It would be of great interest ecologically to determine the coefficient for the same plant under different conditions. Such investigations do not seem to have been carried out; though Briggs and Shantz have determined the "relative water requirement" of different plants under the same set of conditions (1914). Some of their results are set out in Table XXI.

TABLE XXI

(Experiments carried out at Akron, Colorado.)

Plant.	Water Requirement $= \dfrac{\text{transpiration}}{\text{dry substance}}$.
Maize	315–413, mean 368
Wheat	473–559, ,, 513
Rye	502–578, ,, 534
Oats	559–622, ,, 597
Sugar	— ,, 397
Potatoes	554–717, ,, 636
Beetroot	— ,, 743
Peas	775–800, ,, 788
Red clover	— ,, 797

In a more recent paper Shantz and Piemeisel (1927) have summarized the effects of climate on transpiration over the years 1911 to 1917.

The methods discussed up to the present aim at the investigation of transpiration as an ecological process, that is, the effect of external conditions upon transpiration, and the interaction of transpiration with the gas exchange of assimilation and the growth rate of the plant. Reference must now be made to methods whereby the water balance, i.e. the ratio, water uptake/water loss, can be measured. As has been mentioned already, there are serious difficulties in the way of making such measurements, since it is impossible under

natural conditions to determine directly the speed of uptake of water by the roots. Beside the method of Livingston, which has been mentioned on page 122, there is another method which depends on the observations of Kraus upon the alterations of turgor in the plant cell (1881). Kraus discovered a daily periodicity of turgescence which reflects exactly the changing water balance. McDougall has described how the trunks of trees swell at night when the water uptake from the roots is greater than the transpiration, and shrink during the day when the transpiration is greater than the water uptake, and he has constructed an automatic "dendrograph" to measure this (1924). Bachmann (1922) has succeeded in measuring these changes of turgescence with his automatic "Hebelpachymeter."

The lower limit of the water balance—the wilting coefficient—has naturally no definite position, since it varies with a host of other factors which determine the rate of uptake of water and the transpiration. It is sounder to confine oneself, as Shull has done, to the determination of the pressure in the soil against which the roots have to work. (*See* Briggs and Shantz, 1911; 1912; Caldwell, 1913; Livingston and Shreve, 1914; V. H. Blackman, 1914; Russell, 1921.) The hygroscopicity, discussed on page 114, is some measure of the power with which the last traces of water are held in the soil.

In 1913 Crump put forward a simplified method for the determination of the available water in the soil. He determined the quotient water/humus in air-dried soil and found it fairly constant, from which he concludes that it is largely the water held by the humus which is not available for the plant.

In order to evaluate the significance of the water minimum in the soil for ecology, it is very important to know the extent of the root systems of plants in the soil. Very often the upper layers of the soil are completely dry, while at greater depths adequate water is present; so that the wilting-point will differ for different depths. Weaver's investigations (1919; 1920) of the extent of the root systems in arid prairie soils are of particular interest in this respect. Out of 43 species in a typical prairie in Nebraska, 65 per cent had very deeply penetrating roots (from 5–20 feet), and only 14 per cent had their roots in the upper 2 feet of the soil. The rainfall reaches only 28·6 inches per annum, and in summer the upper layers of the soil dry out. Deeper down, however, there is always enough water present.

PLATE V
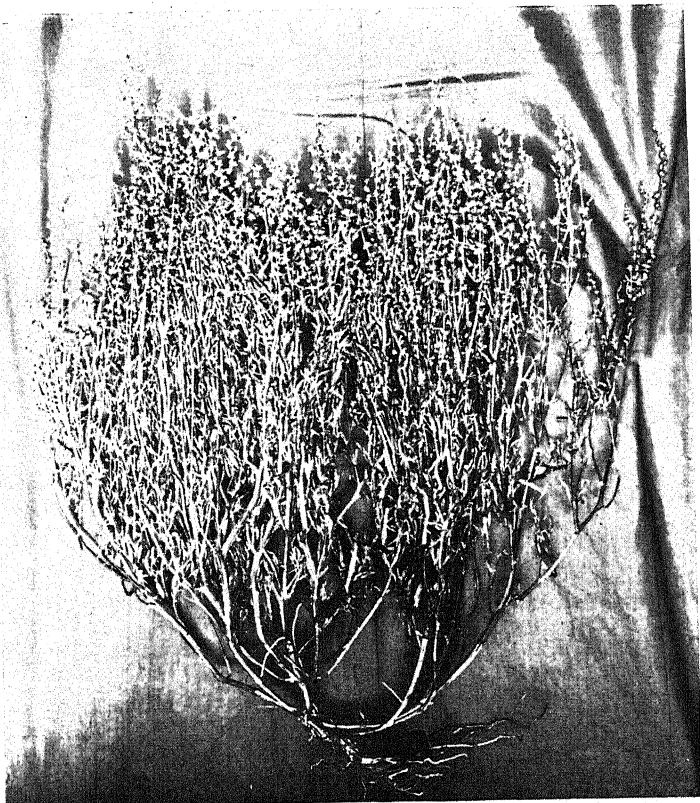
(a) *Atriplex litoralis* from seaweed beds. Notice the weak development of the root compared with the shoot system.

(b) Luxuriant vegetation of *Atriplex litoralis* from seaweed beds in a creek.

Several investigations have been carried out upon the extent of the root system in desert plants (Cannon, 1911; 1913; 1918, *a*; 1918, *b*; Markle, 1917; Fitting, 1911). According to Cannon, certain succulents, especially the cacti, are distinguished by a superficial root system. The roots of other desert plants can penetrate to extraordinary depths; in fact the majority of desert plants seem to possess a very extensive root system, both vertically and horizontally.

From these considerations it is obvious that, for an examination of the water minimum from the point of view of ecology, a knowledge is necessary of the water storage, and the conduction of water through the whole volume of soil reached by the roots.

As a counterpart to the determination of the water content of the soil, is the measurement of the saturation deficit of the air, which, together with the temperature, determines the physical transpiration rate (Bolas, 1926). This saturation deficit can easily be calculated from tables, though it is often more convenient to measure directly the evaporation from a free water surface, by means of an evaporimeter, or atmometer (Livingston and Shreve, 1921; Benecke-Jost, 1924). The extent to which transpiration is purely physical can be observed by putting atmometer and plant side by side, so that both are influenced by the same conditions. The atmometer values, naturally, do not record deviations from the theoretical transpiration due to changes in the aperture of the stomata; moreover the atmometer is not influenced by radiation and by wind in the same way as is the plant (Hüber, 1923). Evaporimeter measurements, if employed cautiously, will, however, give interesting information as to the gross effect of climatic factors on transpiration, and as to the variation of these factors over small areas (Walter, 1928). American investigators, especially Livingston and his school, have often observed a parallelism between evaporation and the distribution of vegetation (Fuller, 1914; 1923; Thone, 1922; 1924; Gates, 1926). Szymkiewicz (1923–6) has drawn certain conclusions as to the significance of humidity for the distribution of plant societies, from measurements of the saturation deficit of the air.

The value of the "relative transpiration" (the ratio: transpiration/evaporation) gives, according to Livingston, some insight into the regulatory action of the plant itself. For this ratio, it is necessary to estimate the transpiration per unit leaf area. The transpiration per unit weight of the plant

gives some idea of the water economy, and the degree of
xerophytic adaptation in the plant (Stocker, 1928).

5. ADAPTATIONS TO THE WATER FACTOR

(a) **Anatomical Characteristics.** Rippel (1919) grew
Sinapis alba in two soils, respectively at 25 per cent and
55 per cent of their water capacities. Except for this differ-
ence in the water content of the soils the two sets of plants
were under identical conditions. The plants in the drier soil
were smaller, but had more "veins" to the leaves, and more
stomata than the plants in the damper soil. Under conditiɔns
promoting transpiration the former plants lost more water per
unit leaf area than the latter, though in shade this condition
was reversed. Apparently the position of the transpiration
optimum differs for sun and shade plants, just as the shape of
the assimilation curve differs. Hüber emphasizes, too, that
shade leaves are more sensitive to changes in water supply
than are sun leaves.

Beside the functional adaptations to the conditions of the
habitat, there are, as might be anticipated, genotypic differ-
ences in the anatomical structure, and in the transpira-
tion rate, which would remain specific in different plants,
even when they are brought under the same conditions
(Blagowestschenski, 1926; Turesson, 1927; 1928).

(b) **Regulation of Osmotic Pressure.** When the
same species develops on both a dry sandy soil and a wet clay
soil, the individuals show a marked regulation of the osmotic
pressure (Pringsheim, 1906; Iljin, 1916). The plant on the
dry soil develops a higher pressure in the roots and the leaves
than the plant on the wet soil. The following table illustrates
this point:

TABLE XXII

REGULATION OF OSMOTIC PRESSURE IN ROOT CELLS. (Iljin.)

Water Content in Percentage of Water Capacity.	Osmotic Pressure in $\frac{N}{1}$. NaCl.	
	Helianthus annuus.	*Zea mays.*
80%	0·14–0·16	0·17
60%	0·25–0·28	0·19
30%	0·41–0·45	0·49

Probably the regulation depends upon the minimum values of the water content, and not upon the mean values given above. Similar results were obtained by a comparison of the osmotic pressures of a number of typical meadow and steppe plants (*Poa pratensis*, *Festuca ovina*, *Koeleria gracilis*, *Stipa capillata*, etc.), some of which were growing on meadows, and some on steppes. The individuals growing on the steppe had throughout higher osmotic pressures.

When the water is held in the soil by the osmotic pressure of soil salts, suitable "adaptations" are to be found in plants to overcome this back pressure. It is a phenomenon which can be studied in the halophytes, where an increase in the salt concentration of the medium produces a corresponding increase in the internal osmotic pressure, so that the internal osmotic pressure always remains higher than that of the medium. Some experiments in which the writer grew *Honckenya peploides* in solutions of common salt, demonstrated that the adaptation takes place through uptake of salt. Some results are set out in Table XXIII (Lundegårdh, 1919, *b*).

TABLE XXIII

Concentration of Salt.	Salt Content of Plant after a Fortnight.
0·0% NaCl.	1·16% chloride.
0·5% ,,	2·09% ,,
2·0% ,,	3·49% ,,
4·0% ,,	6·83% ,,

In *Atriplex latifolium*, too, a similar regulation occurs; but it appears in this instance that the regulation of osmotic pressure does not consist solely in the uptake of a corresponding amount of salt, for the concentrations of other substances in the cell sap were observed to alter. More recently Poma (1922) has obtained similar results; he has found that by increasing the osmotic pressure of the culture solution in geometrical progression, the osmotic pressure of the cell increases in arithmetic progression. (*See also* Brieger, 1928).

The plasticity of species toward changes in osmotic pressure varies widely. The halophytes seem to be the most plastic; this may depend upon the fact that their plasma can

endure the high salt concentrations necessary for the generation
of high osmotic pressures within the cell. Mangrove plants,
too, attain very high osmotic pressures; in *Avicennia officinalis*,
at low tide, Faber has measured a pressure of 163·2 atmos-
pheres in the leaves, and 96 atmospheres in the roots. At high
tide the roots were surrounded by a solution which contained
from 8 to 12 per cent of salt.

In higher latitudes the seas have a lower salt concentra-
tion, on account of the lower evaporation rate of those regions.
Most obligate halophytes, however, are surrounded at high
tide by undiluted sea water. The writer has determined the
osmotic pressure of a number of plants which grew on the
shore of Hallands-Väderö in Kattegat (Lundegårdh, 1919, *b*).
These observations are set out in Table XXIV.

TABLE XXIV

THE OSMOTIC PRESSURE OF NORTHERN HALOPHYTES

Plant.	Tissue.	Pressure in Atmospheres.
1. *Atriplex latifolium* .	Mesophyll and epidermis	29·3–37·0
2. ,, *litoralis* . .	,, ,, ,,	〉37·0
3. *Aster trifolium* . .	Epidermis	26·8–32·1
4. *Spergularia salina* . .	Mesophyll	29·4
5. *Glaux maritima* . .	Mesophyll	20·2–29·3
6. *Salsola kali* . . .	Mesophyll and epidermis	25·9–30·6
7. *Honckenya peploides* .	,, ,, ,,	12·9–18·5
8. *Armeria elongata* . .	,, ,, ,,	18·5–27·7
9. *Scirpus maritimus* . .	Mesophyll	22·2
10. *Rumex crispus* . .	,,	18·5
11. *Solanum dulcamara* .	,,	18·5

There is a definite relationship between the osmotic pres-
sure and the habitat of the plant. Numbers 1 to 4 grow in the
lowest littoral zone, where the roots are periodically covered by
the sea. *Honckenya* only grows as low as the upper limit of the
high-water zone, while *Rumex* and *Solanum* occur only in the
upper supra-littoral zones.

In deserts where the salt concentration around the roots
can rise very high, there are sometimes to be observed extra-
ordinarily high osmotic pressures (Fitting, 1919). The
osmotic pressure of the soil will naturally depend, not upon the
salt content per unit weight of soil, but upon the concentration

of water in the soil.   In a dry soil, therefore, a small amount of salt can generate a high osmotic pressure.   In the lower super-littoral zone of a sea-shore, for example, the writer found after a long drought, that the water content of the soil was 550 mg., and the salt content 6·8 mg., per 15 cc. soil.   The salt concentration of the water was, therefore, about 1 per cent. After rain, this concentration vanished rapidly.   Work of Iljin has shown (1916) that dryness of the soil produces a zonation of plants according to their osmotic pressure.

That this regulatory increase of osmotic pressure is an adaptive modification, which ensures the safety of the water balance, there can be no doubt.   Over the details of this regulation we have, up to the present, very little information. Results obtained by Pringsheim (1906), Stange (1892), and the present writer (1919), suggest that every species has a definite normal pressure, and that satisfactory regulation is more difficult, the further the outside pressure stands from this normal.

(c) **Water Storage.**   Increase of osmotic pressure is not the only way in which plants ensure their water balance; and the succulents provide an excellent example of another method.   The succulents exhibit throughout a strikingly low cell sap pressure.   According to Livingston (1906), the cell sap pressures of *Cereus* and *Opuntia* reach no more than 5·5 to 5·9 atmospheres.   Values as low as 0·4–0·5 normal KNO_3 have been found by Fitting (1911) for *Opuntia*, and Falck (1913) has recorded values of 0·2 normal KNO_3, corresponding to 7 atmospheres, for *Sedum acre*, *S. album*, and *S. rupestre*.   Pressures of the same order, 5·5–6·7 atmospheres, have been found by the writer (1919, *b*) for *Sedum maximum*. Even the halophilous *Sueda maritima* has a pressure of only 7·5 atmospheres.

In the succulents, then, the water balance is not ensured by a high suction pressure.   During the dry period the uptake of water is suspended.   To replace this the plant draws upon a reserve in its tissues; and since transpiration during this time is cut down, the reserve is sufficient to tide the plant over the dry period.   Since succulents are able to endure severe wilting, they are able to use up this water reserve almost completely.

(d) **"Xerophytism."**   A characteristic of xerophytes seems to be an extensive resistance to wilting.   According to Livingston and Brown (1912), plants in the Arizona

desert lose in the dry season up to 8 per cent of their water. Maximov (1924) found for *Artemesia*, *Zygophyllum* and other xerophytes on the steppes at Tiflis a transitory water loss of from 20 to 25 per cent. In extreme cases the upper leaves remove water from those below, and the latter wilt first. Mesophytes, on the other hand, wilt when the water content has fallen 1 per cent (Knight, 1922).

Stocker (1928) has published data which show that desert plants may transpire more per unit surface area than ordinary mesophytes in Germany. Even the stomata of desert plants are open for a surprisingly long time during the day. Since, in the xerophytes, the ratio: surface/water content, is always very low, the transpiration per unit fresh weight is considerably below that of the mesophytes. This is undoubtedly a morphological adaptation for reducing the water requirements of the individual plants.

There are obviously many different methods of adaptation to inadequate water supply; and in recent years we have progressed far beyond Schimper's conception of xerophytes. In the light of modern research one can support Stocker in his attack upon expressions such as "xeromorphic," "xerophilous structure," and so on, since they do not cover the concept of xerophyte at all completely.

Very great restraint must be exercised in providing a physiological interpretation of form and structure. The halophytes, for instance, on account of their succulence, were formerly considered to be typical xerophytes (Schimper, 1898). The work of Delf (1911) has shown, however, that *Salsola*, *Sueda*, and *Salicornia* transpire as freely as mesophytes. In mangrove plants, too, Faber (1912; 1923) has observed vigorous transpiration.

Recent investigations of Stocker (1924) have shown that the transpiration of *Atriplex hastatum*, *Salsola kali*, *Honckenya peploides* and *Cakile maritima* is of the same order as that of typical mesophytes such as *Galium mollugo* and *Heiracium umbellatum*. The succulence of such plants is only useful to them in that it enables them to tide over brief periods of drought. The degree of "xerophytism" of the plant cannot be judged from outward appearances. The form, size and position of the leaves, and the number and size and regularity of the stomata are all of significance. For a description of this subject, the reader is referred to Renner (1910).

Consideration must also be taken of the efficiency of the

conducting system. According to Zaleski, sun leaves have a thicker network of "nerves" than shade leaves (1902). Water plants have 100–143 mm. of conducting tissue per square centimetre of leaf area, and shade plants in damp woods have 170–340 mm. *Fragaria vesca*, on the other hand, has 648 mm., and in various xerophytes the amount of tissue may vary from 860 to 1,450 mm. (*See also* Farmer, 1918; Schuster, 1908.) A recent publication by Hüber (1928) describes a certain balance of resistance within the plant, so that in a tree, for instance, the lower branches are not "favoured" at the expense of the upper branches. The "specific con-ductivity" of the stem is smaller in evergreens and "xero-philous plants" than in deciduous trees and shade plants, but the limiting factor in water economy is, according to Hüber, the suction pressure. To ascertain the degree of xerophytism of the whole plant it is necessary, as has been made clear above, to know the state of the water balance, and the degree of resistance to wilting.

Even the moorland plants, the *Ericaceae*, have been shown by Boysen-Jensen (1917), Montfort (1918–21–22) and Stocker (1923–4) to be mesophytes or hygrophytes. A "physiological drought," in the sense in which Schimper used the expression, does not exist on moorland soil. On the other hand, moorland water has an inhibitory effect upon the uptake of water by plants unaccustomed to moors, which is expressed as a poison effect.

Recent work has undoubtedly given a very complex and involved conception of xerophytism. We are only at the beginning of this work, but it is quite clear already that xero-morphy by no means presupposes xerophytism in the ecological sense.

Stocker (1923–4) and Stålfelt (1924) have suggested that the xeromorphic structure of moor and heath plants, and of conifers, can be considered as a protection against the mechanical action of wind.

A xeromorphic structure of the leaf, combined with a high stomatal number, would enable the leaf to transpire freely in summer; and in winter, if the stomata are closed, as they are in the conifers, such a structure would provide a protection against transpiration, a protection which is essential for the existence of an evergreen flora when the ground is frozen. The xero-morphy of evergreens, then, is a sort of seasonal xerophytism, and is a counterpart to the formation of special over-wintering

organs in other plants. On account of the mechanical strengthening of the leaves, the ratio of chromatophores to dry weight of the leaf is low; and the leaves of conifers assimilate markedly less per unit area than do those of mesophytes. As a compensation, however, conifers have a far greater relative leaf surface, and their total transpiration in summer is about as high as that of a deciduous tree.

Ivanoff has recently mentioned that in most instances southern species transpire more vigorously than northern species (1924). The conifer with the lowest relative transpiration, *Abies Sibirica*, has the most northerly distribution. Its transpiration, compared with that of the larch as unity, is only 0·3.

The drying out of the plant in winter, especially in connection with strong winds, is a factor of the greatest ecological significance (Walter, 1925–26; Braun-Blanquet, 1928). The observations of Kihlmann (1890) in Russian Lappland show conclusively that the dry winds in frosty weather determine the polar tree limit. Trees on the tundra are no higher than the protective snow layer in winter. Every shoot which grows above this level in the spring, perishes in the following winter; and as a consequence the trees assume a peculiar table-like form.

Similar phenomena are encountered in lower latitudes, on the sea coast (Lundegårdh, 1916, *a*). Especially on the west coast of England it is a common sight to see trees distorted into strange shapes by the prevailing winds from the sea (Plate VI).

The velocity of the wind increases with height above sealevel, as the figures in the following table show. The figures are taken from Stevenson and Hellmann (1919).

TABLE XXV

INCREASE OF WIND VELOCITY WITH INCREASING HEIGHT

Height	.	.	0·05	0·5	8·0	3·0	6·0	9·0	12·0	15·2 metres
Velocity of wind	.	1·04	1·95	2·43	2·4	2·5	2·5	2·5	2·6 m./sec.

This alone would cause a reduction in the height of trees. It is also of interest that, according to Hüber (1923), transpiration decreases with the height above the ground. The lower twigs of *Sequoia* transpire six times as much as twigs 36 feet high. Along certain sea coasts, beech trees, oaks, and limes are crippled at a height of a few metres from the ground. Bushes, such as *Prunus spinosa*, *Cotoneaster*, even junipers, grow

only a foot or two above the ground. When the forest in a
closed formation extends as far as the coast, the height of the
trees gradually decreases, until the outposts near the coast are
no more than little bushes, like the dwarf willows at the Alpine
or the Arctic tree limit. Not only the trees, but even the ground
flora suffers under the influence of a sea wind. There is a com-
pete elimination of tall or brittle species. The greatest influence
of wind is found in climates where the saturation deficit is high.
Stocker has stated that in the North African desert there are
wind storms of 13 metres a second, over soils at 37° C. and
only 2 per cent humidity. In the Alps, too, the wind has a
significant effect upon vegetation (Braun-Blanquet, 1928).

6. THE SIGNIFICANCE OF THE WATER FACTOR IN PLANT GEOGRAPHY

Of the 1,340 million billion Calories which stream into the
earth's atmosphere every year (Schroeder, 1919), fully one-
quarter are used up in the evaporation of water. The
evaporated water follows the air currents, is condensed as rain,
and deposited on the continents, which otherwise could not
support vegetation at all. The distribution of rainfall over
the earth is very varied. In the following discussion the
work of Hann on this subject (1915) has been used as a source.

TABLE XXVI

Latitude	N. 70°	60°	50°	40°	30°	20°	10°	0°	10°	20°	30°	40°	50°S.
Rainfall, in cm. over land	21	44	48	46	51	52	137	**193**	151	79	52	58	79

The heaviest annual rainfall is to be found on the Equator.
Toward the Poles the rainfall decreases. In sub-tropical
zones there is a minimum at about 30°, though this does not
occur in the table given above. At this latitude the rainfall in
the interior of continents is very small, often not exceeding
25 cm. It is a region of steppes, savannahs, and deserts, in
the northern hemisphere, in Africa, and Arabia and Mexico;
in the southern hemisphere in South Africa and America, and
on the west coast of Australia. For maps of the distribution of
rainfall the reader is referred to Bartholomew's Meteorological
Atlas.

In India, on the other hand, on the same latitude as the
Sahara and Arabian deserts, are to be found very rainy fruitful
regions. This is due to the monsoons, which in the course of

the summer, spread the moisture from the Indian Ocean over the southern part of the Indian continent. In winter the monsoons blow from the continent towards the sea, and at this time of the year the dry season occurs. To the north the Himalayas throw a huge "rain shadow"; on the southern side of the Himalayas the highest rainfall on the whole earth has been recorded (an annual mean of 1,163 cm. is recorded for Cherrapunji), while to the north lies the desert of Tibet.

In the temperate zones the rainfall is fairly evenly divided throughout the year, and depends to a great extent upon a succession of depressions travelling from west to east across the continents. Owing to the prevailing west winds, the west coasts of the northern hemisphere have a higher rainfall than the east coasts. Styehead Pass, in Cumberland, for instance, has the highest rainfall in Europe. In the tropics this state of affairs is reversed; the east sides of islands and continents have the greatest rainfall, owing to the prevailing trade winds, which blow from the east.

On account of the rain shadows cast by mountain ranges, and for other reasons, the rainfall usually decreases from the coast inwards, and this decrease is accompanied by a concurrent zonation of the plant life, from mesophytic to xerophytic. In some regions, however, the cyclones penetrate to great distances into the continents, and the regions reached by the cyclones enjoy a greater rainfall than they would normally receive.

Beside the mean annual rainfall, attention must be paid to the periods over which this rain is precipitated, and to the type of the rain, whether it is fine or heavy; it makes a very great difference whether 20 mm. of rain fall in five minutes or in the course of a day. Snow may act as a protection against cold and the drying out of the plants, though too great quantities of snow are able to damage trees by breaking down their branches (Vestergren, 1902). It is obvious, too, that the effect which rain has upon plant life will depend upon the temperature of the climate in which it falls, and upon the constitution of the soil. Some of Hann's figures upon the annual rainfall in different parts of the earth are given in Table XXVII. The figures refer to thousandths of the annual rainfall in millimetres.

Köppen (1923) attempted to classify climates, basing his classification upon the temperature, and the distribution of the

TABLE XXVII

	Tropics						Sub-Tropics		Temperate Zone			
	Double Rain Period		Single Rain Period				Winter Rain Period		Continental Summer Rain		Coastal Regions	
	Equatorial											
	South Africa. 6° S.	Quito. Equator.	South Border of Sao Paulo. 23° S.	North Tropics. Mexico. 19° N.	Trade Winds. Hawaii. 20° N.	Monsoons. Port Darwin. 12° S.	West Australia. 32° S.	South Italy. 38° N.	Cent. Europe. 59° N.	North Asia. 55° N.	North America. 40° N.	N.W. Europe. 60° N.
Jan.	86	77	195	7	79	241	14	130	57	20	84	100
Feb.	80	92	156	9	94	215	18	93	56	17	77	80
Mar.	123	115	103	26	86	166	30	98	68	18	85	72
Apr.	195	169	58	26	94	61	64	75	71	35	70	56
May	91	109	60	85	66	23	150	35	92	75	80	58
June	10	35	46	174	55	1	183	23	115	133	81	64
July	7	25	19	180	82	0	168	8	121	235	96	70
Aug.	17	52	31	207	81	2	166	28	117	215	87	80
Sept.	37	60	60	179	73	5	93	73	82	122	84	102
Oct.	61	91	82	79	88	38	59	133	75	58	91	110
Nov.	188	94	74	20	95	72	32	144	74	40	86	102
Dec.	105	85	116	8	107	176	23	160	72	32	79	106

rainy periods. He distinguished the following eleven climate types, and five main zones:

Zone.	Climate Type.
I. Tropical rainy climate	Tropical rain forest. / Savannah climate.
II. Dry climate	Steppe climate. / Desert climate.
III. Warm temperate rainy climate	Warm climate, dry in winter. / Warm climate, dry in summer.
IV. Boreal, or snow forest climate	Climate with cold and dry winters. / Climate with cold and damp winters.
V. Snow climate	Tundra climate. / Climate of eternal snow.

The system is further subdivided by Köppen, but it will be sufficient to discuss here some of the types listed above, in so far as they determine the distribution of vegetation.

(*a*) **The Tropical Rain Forest.** In the equatorial zones are to be found the tropical rain forests, which form a belt round the earth. The conditions for the uninterrupted vitality of these forests are the high equable temperature, and the rainfall equally distributed throughout the year, a condition which obtains especially in the region of the trade winds. The generally favourable conditions make no demand upon the plasticity of the species; there is no call for extreme competition forms. Here perhaps lies the indirect reason for the extraordinary wealth of species and the diversity of life forms in these regions. Furthermore, as might be expected under such conditions, there are many variants of the tropical rain forest, due to small differences in the soil or in the historical development (*see* Schimper, 1898; Warming-Gräbner, 1915–18; Shreve, 1914; R. C. McLean, 1919).

Despite general uniformity of climate, plants in the higher "layers" of a rain forest live under widely varying conditions, especially of humidity. Humidity exhibits a wide range of daily variation (McLean, 1919). According to Haberlandt's investigations (1898), the humidity in Java decreases as the sun rises from 6–7 in the morning until 1–2 in the afternoon. (*See also* Stahl, 1894.) At the end of this period the saturation deficit of the air is often as low as 30 per cent; while during the remainder of the day the relative humidity is from 93 to 95 per cent. It is scarcely surprising, then, that most of the trees in a tropical rain forest have leathery leaves. Similar

conditions have been described by Shreve, for the montane rain forest in Jamaica (1914) (Fig. 54), and by McLean for the forest of Rio de Janeiro (1919).

As a result of this marked decrease in the relative humidity, together with an intense insolation, the transpiration curve of plants in rain forests rises to a high level during the forenoon. There is some difference of opinion regarding the comparative intensity of transpiration in the tropics and in cold temperate
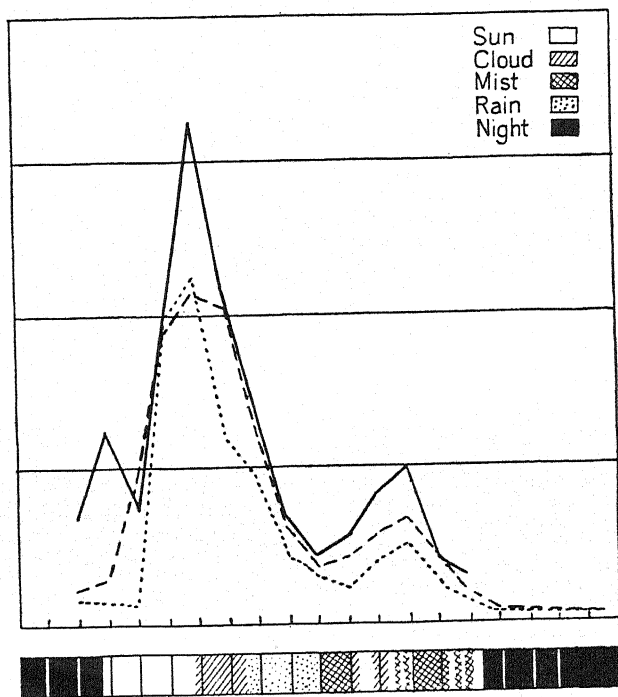
FIG. 54.—Daily course of transpiration in *Clethra* (——————) and *Alchornea* (··············), together with the corresponding evaporation rates (——————) in the Jamaican rain forest. Below: the weather changes during the period. (After Shreve, 1914.)

zones.   In Jamaica Shreve found, in eight different plants, minimal values varying from 11·08 in *Dodonia angustifolia*, to 1·58 in *Pilea nigricans*, measured as milligrams per square centimetre of leaf surface, values which are not far out of the range of those found in Europe.

This marked rise of the midday transpiration is, however, of relatively short duration, for in the afternoon the rain showers set in.   The degree to which the stomata react to this

midday sinking of the water balance, and the consequent effect upon the assimilation, remains yet to be discovered. It might be conjectured that the sclerophyllous structure would afford some protection.

Shreve has compared his values for the relative transpiration (i.e. transpiration/evaporation) with those obtained by Livingston and Edith Shreve for desert plants in Arizona. He finds that the most xerophytic rain forest plants, the trees, have about the same transpiration as the most hygrophilous desert plants.

It would appear, then, that the plants of a rain forest have no remarkably high transpiration. In the lower levels of the forest, of course, daily fluctuations in humidity, temperature and insolation become equalized, and on the floor of the forest extreme hygrophytes flourish, such as the *Hymenophyllaceae*, with their filmy leaves.

From the standpoint of ecology the tropical rain forest is a very complicated formation. It consists of upper regions in which the water factor, the light and the temperature factor vary within wide limits. Below, on the floor of the forest, there live extreme hygrophilous shade plants, in a climate with subdued light, and with none of the fluctuations of humidity, temperature, and movement of the air which characterize the climate of the upper regions; and between these two extremes there is every grade of intermediate conditions.

(*b*) **Tree Steppes and Savannahs.** Within the tropics there exist numerous transition formations between rain forest and desert, known under the names of monsoon forest, savannahs, thorn forest, semi-desert and so on. These occur where, on account of the high evaporation, the rain is insufficient to keep the ground constantly wet, and where a dry period of several months occurs (Table XXVII). To quote Schimper (1898, p. 303): "With a minimum rainfall of 180 cm. rain forest prevails; with a rainfall between 90 and 150 cm., xerophilous wood and meadows enter into competition; below 90 cm., a xerophilous undergrowth, especially thorn wood and thorn bush, occur, merging at still lower rainfalls into semi-desert and desert." Such a classification according to annual rainfall is naturally very schematic, since the evaporation and the annual distribution of the rainfall also come into play; in essentials, however, it may be regarded as accurate.

The tree steppes or savannahs occupy extensive regions on both sides of the Equator, in South America (Warming,

1892), in Africa (Engler, 1908–16), and in Australia (Warming-Gräbner, 1915–18). In the dry periods the trees lose their leaves. Closed woodland formations occur only in the coastal regions, where the climate is more moist. The typical tree-steppe takes the form of meadows of tall stiff grasses, whose vegetative development is completed in the rainy season, and which are already in fruit when the dry season arrives, bearing an analogy in this respect to the northern steppe grasses. Scattered in the meadows, at some distance from one another, are trees, which for the most part are xeromorphic —*Adansonia digitata*, for instance, the tree-like *Euphorbias*, and the African acacias, and the species of *Eucalyptus* in Australia. Bushes with a highly developed root system are also characteristic of this formation.

On account of the inadequate rainfall of these semi-arid zones, a change in the water capacity of the soil or in its permeability are markedly reflected in the character of the vegetation. Meadow and savannah flourish on a heavy soil, where the water remains in the superficial layers. A pervious soil, like sand, promotes the growth of trees, for the evaporation from the soil is less, the water penetrates to deeper layers, and is available in the dry season—a fact which is of great importance for trees. The character of tree-steppe, therefore, varies between meadow and woodland, according to the nature of the soil and the amount of rainfall.

(*c*) **Deserts.** For the descriptions of the morphological and anatomical adaptations of desert plants against the unfavourable conditions of water balance in deserts the reader is referred to the works of Schimper (1898) and Warming (1918). The physiological peculiarities of desert plants were touched upon in the discussion of xerophytism on page 137. It was discovered that the evolution of the genotype has progressed along two paths. The first is represented by the succulents (of which the cacti have been most thoroughly investigated), where the water balance has been preserved by a reduction of the transpiration, and by "pentosan metabolism," i.e. the building up of tissue of high water-storing capacity; while there is no high suction pressure developed. (*See also* Shreve, 1924; Blackman, F. F., 1921.) The second type of desert plant develops a suction pressure higher than the "back pressure" of the ground in which it grows, or develops a root system which penetrates very deeply into the soil.

The transpiration of real desert plants is still incompletely understood. It seems from the investigations of Livingston (1906) and E. Shreve (1914), that their transpiration is greater than one would expect from their xeromorphic structure. In the desert, water is the factor in absolute minimum, and it is quite dominant over other factors in determining the vegetation, although under such conditions movement of the soil, as happens in dunes, may affect the vegetation profoundly.

The transition from a region of high rainfall to one of low rainfall, from savannah to desert, is gradual, but it must be remembered that directly the vegetation ceases to cover the ground in a continuous layer, the ground loses a sort of blanket, and the evaporation from the soil increases enormously. It is a well-known fact that a soil covered by plants is warmed less by radiation, and has a lower evaporation, than a bare ground; this is a phenomenon which has been particularly noticed in woods, where a covering of moss can increase the water content of the soil by 30 to 40 per cent (Albert, 1915). In the tropics the differences are still bigger, so that in the desert most of the rain water is evaporated again, without benefiting the plant at all.

(*d*) **Sub-tropical Regions.** The tropical deserts occupy an area on either side of the tropics, a region which in Asia is continuous with the temperate deserts. Outside these regions are zones with a somewhat higher rainfall, which are transitional to the cold temperate regions of moderate humidity. The increase of humidity with increasing latitude is due to the progressive decrease in evaporation. Naturally one gains no idea of this from an inspection of the mean values for rainfall. This influence of evaporation intensity upon water, as an ecological factor, accounts for the marked difference between regions with summer rain and dry winter and regions with winter rain and dry summer. Given equal rainfalls in the two regions, the former are the drier.

When the rainfall is heavy, and more or less evenly distributed over the whole year, the last outliers of "rain forest" in sub-tropical zones are to be found, in Florida, for instance, in India and Japan. These temperate rain forests occupy only a few restricted regions; their character alters as the latitude increases, an alteration which can be attributed to the influence of the temperature factor.

(*e*) **Mediterranean Vegetation.** The so-called Mediterranean climate, with its rainy winters and dry summers, is

specially characteristic of the warm temperate zone.   The soil
of these regions is not able to retain through the summer the
rain which falls during the winter, so that the climate is not a
good one for woodland.   The dominant trees are xeromorphic
and sclerophyllous, such as *Quercus ilex*, *Olea Europea*,
Laurus nobilis, and *Pinus pinea*.   Other formations character-
istic of this climate are the "garigues" and the "macchia"; the
former an open formation of typical Mediterranean bushes,
shrubs, bulbous plants and annuals, and the latter a closed
formation of bushes and small trees.   Since their time of
vegetative development is not in the summer, these forma-
tions are in this respect contrasted to the steppe formation.
The principal developmental period is in the spring, but by
reason of the mild climate growth can take place in the winter
too.   In fact the northern limit of the Mediterranean vegeta-
tion is really determined by the frost line, north of which
winter growth is inhibited.   In the cooler climate of the
steppes this winter period of growth cannot occur.   The thin
leaves of deciduous trees in such a climate would wilt during
the summer; so that the characteristic tree vegetation is the
broad-leaved sclerophyll type.

    A recent paper by Guttenberg (1927) confirms these as
general characteristics of the Mediterranean flora.   He found
the period of greatest assimilation of sclerophyllous leaves to
be in the spring, when the ground is moist, and the stomata
are open all day, in both sun and shade.   During this period,
from March to April, the plant stores starch against the dry
summer, when photosynthetic activity is suspended on account
of the closure of the stomata.   In assessing the value of
Guttenberg's work, it must be mentioned that the method he
employed for determining assimilation is somewhat crude.

    (*f*) **The Cold Temperate Deciduous Forest.**   South
of the Alps the Mediterranean climate prevails.   North of the
Alps the conditions are totally different; rain falls throughout
the whole year, though the rainfall is generally greater in
summer than in winter.   In parts of North America, too, there
is a cold temperate region with a rainfall evenly distributed
throughout the year.   In this climate, which is damp both
summer and winter, the northern deciduous forest is to be
found.   The trees in such a forest are "hygromorphic" in
summer, and in winter, when they have shed their leaves, they
are xeromorphic.

    Trees are particularly interesting for the investigation of

a number of ecological problems. Owing to their size and shape the inner water economy may be very complex; the upper and lower leaves may have very different water contents, and hence different intensities of assimilation. Very little is known of the carbohydrate balance of a deciduous forest.

The forestation of an area changes completely the conditions of humidity for the under vegetation, and creates, in fact, a new habitat. Fuller (1914) and Larsen (1922) have described various American forest types from this standpoint.

(g) **Steppes and Prairies.** For the existence of the deciduous forest the water stored in the depths of the ground is essential, for upon this store the tree draws in summer. When such a store is lacking, the trees disappear, and the formation becomes a steppe. The conditions for the formation of a steppe in a cold temperate climate are: an annual rainfall below 40–50 cm., a dry summer, and a soil of such physical constitution that the rain remains held in the superficial layers (see also Vahl, 1911). The rain falls generally in very heavy storms. On account of the powdery nature of the soil most of the water runs off without penetrating into the ground. According to Ramann (1911), the water capacity of the black soil of Russia can be taken as 25–30 volume per cent. At a very early stage the soil dries out to 10 per cent or less. A rainfall of 10 mm. saturates no more than the upper 5–7 cm. of soil and succumbs easily to evaporation. In the steppe region of Russia the month of the greatest rainfall is June, with 5 to 7 cm. The relative humidity through the summer is 60–70 per cent, but the evaporation is very strong indeed. Nothing more can flourish, therefore, than a xeromorphic vegetation, which develops rapidly, and which draws its water supply from the superficial layers of the soil. By late summer the steppes appear burnt up, and powerful, dry winds blow over them. In the autumn, however, another burst of vegetation appears (Warming-Gräbner, 1915–18).

The plants of the North American steppes, the prairies, are, as described on page 118, very deeply rooted in the soil. The water supply of the soil is more available to the plant than it is on the steppes of Central Russia or Czecho-Slovakia, but it is still inadequate for the growth of trees. The prairie soils of Nebraska and Colorado Springs, investigated by Weaver (1920), in the summers of 1916–18, were never fully dried out at a depth of 5 feet. Briggs and Shantz, however, have

mentioned that in certain years the drying out went as far as to the wilting coefficient. The conditions naturally vary considerably in different years. (*See also* Alway, 1919.)

When water is the factor in absolute minimum, a small change in the annual rainfall or in the evaporation has a marked effect upon the vegetation. Weaver (1920) has given some examples of this. He compared two habitats, the true prairie at Lincoln in Nebraska, and the mixed prairie at Colorado Springs. In the latter habitat the evaporation is significantly greater, while the rainfall is less than that in Nebraska. Consequently at Colorado Springs the general aspect of the vegetation is more xeromorphic. In Europe, too, the physiognomy of the steppe alters with the water factor, though the nature of the relationship has not yet been closely investigated.

Since the absence of trees on the steppes is due simply to a lack of water in the deeper layers of the soil, the vegetation on the borders between regions of high and low rainfall fluctuates between woodland and steppe.

In two districts, where the rainfall is the same, the type of soil may determine the issue. Sandy soils in the steppe regions almost always bear woodland (Ramann, 1911; Kostytschew, 1890). Ototzki (cited by Ramann) has shown that the water table is deeper under woodland than under steppe, from which he concluded that a greater proportion of the rain evaporated before ever it reached the ground. It might also indicate that the trees draw upon the water table to a greater degree than the superficially rooted herbs, whose transpiration is indeed much weaker. On the other hand, since trees protect the open parts of the ground from evaporation, they may serve to increase the water balance in this respect. It is evident that the presence of trees changes completely the moisture conditions of the soil beneath, and may enable a mesophilous ground flora to grow, where, without trees, only a xerophilous steppe flora could flourish, under conditions of much higher evaporation from the soil. On an open steppe, evaporation rises rapidly with height above ground. On a British moor Yapp (1909) found that the evaporation rates at 4 inches, 2 feet, and 4 feet above the ground were relatively 6·6 : 32 : 100. An evaporation rate increasing so rapidly with height, on a dry windy steppe, would well account for the absence of trees, bushes and taller shrubs. As soon as forest has become established, the

humidity near the soil rises at once, and a mesophilous soil vegetation can develop on what was earlier a steppe soil. The trees at the limits of the steppe in Russia are principally oaks, and beneath them there has developed a rich meadow-like vegetation (Rehmann, 1872).

(*h*) **Northern Forest and Bog Formations.** In the deciduous forest climate the water factor is no longer in minimum, and does not alone determine the vegetation. The presence of the dominant plants, the trees, is determined by other factors, such as temperature and the constitution of the soil, while the vegetation under the trees depends upon the soil constitution too, and the intensity of the light. The influence of the water factor, however, is ubiquitous, though it is often difficult to decide how important a part it plays in the plexus of ecological factors. When the intensity of several factors is adequately high for plant growth, the physiognomic aspect of the vegetation is often varied, and the appearance is often as if different types of vegetation could develop under the same set of ecological conditions. In view of the very superficial state of our knowledge of the environment, there is, of course, no justification for such a view, and before any conclusion of any sort could be drawn, the history of the habitat would have to be known.

In general the ground vegetation in an oak wood is different from that in a beech wood or a fir wood; this difference can be shown to depend upon the light, though the constitution of the soil and the humidity also play a part. The occurrence of *Rubus*, *Mercurialis* and *Pteris* in British oak woods, for instance, depends upon the moisture conditions obtaining there (Watt, 1924). The soil itself is really created by the plants which grow in it. The development of such a diverse formation as a wood takes place under a continuous interaction of the plants and their external environment.

Now when the water factor passes into the maximum region, the aeration of the soil is indirectly affected. At this point is reached the upper limit of humidity of the deciduous forest, and forest passes over into extremely hygrophilous vegetation, bogs and moors. The conditions for such formations are decided, not by the rainfall alone, but also by the evaporation and the rate of conduction of water through the soil. Bog formations are frequently found on coastal regions, owing to the high relative humidity and low evaporation. Another cause of bog formation is bad drainage of the soil.

It is not the excess of water which poisons the roots of the trees, but the lack of oxygen, and the surplus of carbon dioxide, especially when the excess of water lasts over a long period. Some trees, however, will endure periodic flooding, as, for instance, those growing in the lowland woods of South-east Europe, and in the alder woods of West Sweden. In the plains of Moravia, the river rises in spring, and floods the fields and the woods, which latter consist mostly of oaks and ash; the river sinks again in summer. In the northern alder swamps, too, the water dries out by summer. The floods in the spring-time are caused principally by the winter ice, which cuts down the evaporation to a marked degree.

Soils which are constantly marshy, and which will not support the growth of trees, are favourable for the growth of plants like *Sphagnum*, which retain the rain-water, and which alter the physical and chemical constitution of the soil in such a way as to inhibit the growth of trees. The formation of a moor is a very slow process, in which the climatic alteration of the water balance is only the first step, and the peculiar conditions of the habitat are created by the biological character of the dominant plants. The geographical distribution of moors shows that they are not determined by the water factor alone, but also by the temperature, which regulates the rate of decomposition of humus. We shall return to this question in the discussion of soils in the next chapter.

(*i*) **The Maritime and Alpine dry limit of Forests.** Where the evaporation in the summer rises too high, there is reached a limit of dryness at which deciduous forest cannot grow. Thus strong and continued sea winds make the growth of trees impossible, although the climate cannot be considered as arid. For this reason there is a "dry limit" of tree growth along the sea coast, in regions which in other respects exhibit a distinct hygrophytic climate (Plate VI). In the mountains a similar limit of dryness exists, dependent upon the wind, which can reach great force. Under these conditions, both in mountains and by the sea, there prevails a typical hygrophytic climate near the ground and, a few yards above, a xerophytic climate. In such habitats the ordinary woodland ground vegetation appears, though in a combination corresponding to the more open conditions of illumination; and this forms the non-halophyte sea shore meadow, and the Alpine meadow.

(*j*) **Meadowland.** The meadow lands of the European plains, and of the United States, are to a great extent products

of civilization, since grazing is sufficient to inhibit the growth
of trees (Vaupel, 1863; Lundegårdh, 1916, *a*).

It is a well-known fact in gardening that grass lawns are
inhibitory to the growth of trees. It has not yet been dis-
covered whether the cause lies in the poor aeration of the soil
under the mat of grass roots, or whether some other factor is
responsible.

There exists a competition between meadow and wood-
land, and the issue of this competition can be decided in one
way or the other by various cultural methods. If the coppicing
of a wood is carried to excess, the local climate becomes drier,
the wind obtains access to the heart of the woodland, and the
trees are "dried out." Meadows formed in this way on the
coastline often change eventually into heaths.

(*k*) **The Sub-Polar Coniferous Zone.** It will have
been observed that the deciduous forest zone is not continuous,
but is broken up frequently into steppes, meadows, moors, and
heaths. The northern tree zone, on the other hand, which
consists of conifers, is quite closed and continuous.

The conifers differ among themselves as to their water
requirements, though among some of them there is a wide
range of plasticity. *Pinus sylvestris*, for example, is found on
the dry sandy plains of Germany and Northern Sweden, on
sand dunes, and in rainy habitats in Norway and Scotland.
Pinus montana grows on dry calcareous soils and on damp
moorland. The spruce seems to be more definitely hygro-
philous; it has forced its way as closed formations toward the
south, and in mid-Sweden it competes against the beech
(Hult, 1881; 1885).

The whole northern zone of the North American con-
tinent is occupied by various coniferous trees; the water
relations of these have been discussed by Warming-Gräbner
(1915–18) and by Nichols (1913; 1914). As a whole the
coniferous trees can live under a very wide range of con-
ditions, a range much wider, in fact, than is possible for
deciduous forests. If one considers the formation as a whole,
the trees exhibit a remarkable plasticity (Livingston and
Shreve, 1921). This may explain the difference between the
continuous distribution of the coniferous forest zone, and the
discontinuous nature of the deciduous forests.

(*l*) **Arctic Vegetation.** The northern limit of the coni-
ferous zone corresponds to the southern limit of the polar
regions. Temperature is primarily responsible for this

PLATE VI

(a) Beech tree whose crown has been distorted by wind.

(b) The maritime limit of woodland at Hallands-Väderö. The outermost alders are reduced to bushes.

frontier of the polar regions; above the frontier the soil is frozen almost continuously. The upper few centimetres of the ice thaw just for a few weeks in the summer. And here, over vast stretches, there is nothing but the moss tundra, northward as far as the perpetual snows. Since the soil is frozen over the tundra region, there is no available water at the depth to which the roots of trees penetrate, so that the northern tree limit is, to some extent, determined by dryness. Even the moss vegetation dries out in winter, unless it is protected by a layer of snow (Pohle, 1903; Karsten and Schenck, 1907).

The tree limit in the Alps, too, is determined by an interaction of the temperature factor and the water factor. This question has already received attention (p. 105).

The Distribution of Vegetation in North America

Enough has been said of the distribution of vegetation over the earth to emphasize the great significance of the water factor; and it is also fairly evident how great a part temperature plays in the delimitation of the great zones of the earth. It is only when one comes to the details that complications arise. The influence of a factor is only clear and unequivocal when the factor is in minimum. Those plant geographical boundaries, which are determined by the transition of the water factor from a minimum to an optimum value, are quite sharp and clear. As examples might be quoted the frontiers between forest and steppe, sea shore, tundra, or Alps. On the other hand, it is difficult to establish any correlation between the water factor and the boundary between two hygrophilous formations, such as deciduous forest and coniferous forest. In this particular case the limits are determined by temperature rather than by moisture relations.

Very great credit is due to Livingston and Shreve, who have taken the trouble to investigate the correlation between the plant geographical boundaries and "isoclimatic lines," over an area as large and diverse as the United States of America (Livingston and Shreve, 1921). These authors constructed a number of "climatic indices" for various factors. The moisture ratio, for instance, is the relationship: rainfall/evaporation; and the values for rainfall and evaporation were taken not from the means alone, but from the figures for rainfall distribution, etc., during the frost-free period. Twelve such climatic indices in all were constructed, and from these indices a

number of isoclimatic lines were drawn. The boundaries between the plant formations were then compared with these isoclimatic lines. The following are some of the more notable results obtained by these authors:

The desert is correlated most closely with the moisture ratio, while the conditions of temperature vary widely. Semi-desert, on the other hand, is more highly correlated with temperature than with rainfall.

The prairies occupy a wide belt from north to south, and cover, therefore, very different zones of temperature; their presence or absence is determined, however, by the rainfall, especially by its distribution throughout the year. The transition from prairie to deciduous forest is indicative of higher rainfall. The moisture ratio of the transition lies somewhere between those of the prairie and the deciduous forest, though the amplitude of the ratio is much less, indicating that the relative humidity has a markedly controlling action. In prairie and forest, on the other hand, the amplitude of the humidity is very considerable. It is probable that the numerous variants of deciduous forest are due to the interaction of the water factor and the temperature factor.

To express the interference and the interaction of the temperature and the water factors, Livingston introduced the conception of the "moisture-temperature index." This index is calculated according to the following formula:

$$I_{mt} = \frac{I_t . I_p}{I_e},$$

where I_{mt} = moisture-temperature index; I_t = the temperature summation, I_p = the summation of the rainfall over a certified period, and I_e = the total evaporation from the standard evaporimeter.

This method of comparing the vegetation map with the map of selected climatic conditions, is naturally only the first step to an exact ecological investigation of any region. Moreover, a number of conditions determined by Livingston and Shreve, the length of the frost-free period, for example, and the number of days with a certain mean temperature, are very different in their actions upon different plants, while other indices, like the "exponential index" of temperature, have no real meaning at all. Only when the ecological factors can be measured and expressed in such a way as to represent their physiological action, will there be any hope of following more
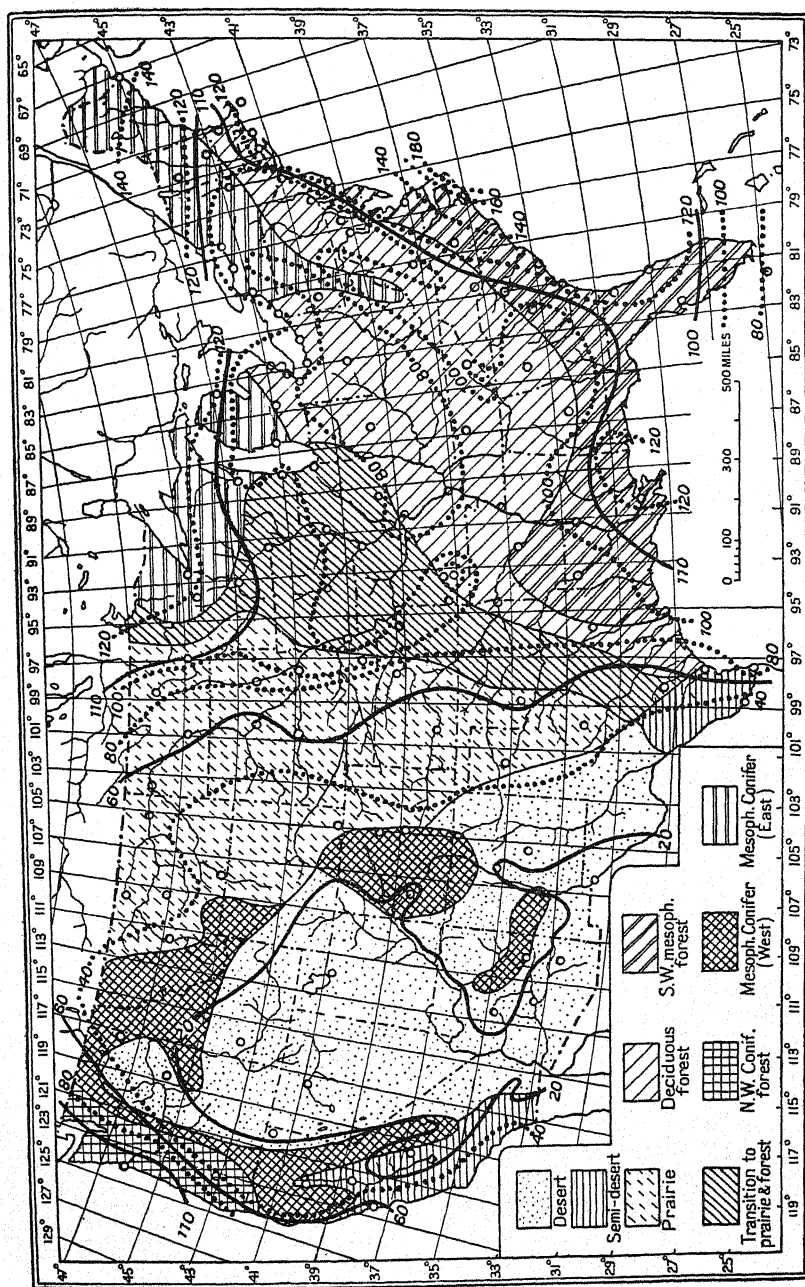
FIG. 55.—Distribution of the principal types of vegetation in the U.S.A. The lines represent the ratio: rainfall/evaporation, for the frost-free period plus thirty days. (After Livingston and Shreve.)

quantitatively the complex correlation between climate and vegetation.   The research of Livingston and Shreve, however, is a piece of pioneer work deserving attention, especially as the authors have taken up a critical attitude to their own results throughout their work.   Their principal result is that the moisture ratio determines as a whole the distribution of formations, a conclusion which is in agreement with those of other plant geographers.

Not only is the gross distribution of plants largely determined by the water conditions, but even their detailed distribution over small areas.   No local climatic differences are so well marked as those due to the water factor, and at almost every yard in a wood or a field there are signs of a transition from hygromorphic to xeromorphic associations.   In a field the water factor takes the place of light in a wood, as a "determiner" for the differentiating of the vegetation.

The following analysis of the sandy shore of Hallands-Väderö will serve as an example of zonation on the sea-shore.

TABLE XXVIII

ZONATION OF VEGETATION ON THE SANDS AT HALLANDS-VÄDERÖ

Water Content up to Air Dry Soil, at depth of 10 cm., 29.6.18 in %.	10·6	2·3	0·4	0·2
Atriplex litoralis	20	—	—	—
Cakile maritima	60	40	—	—
Calamagrostis Epigeois . . .	40	—	—	—
Elymus arenarius	80	60	60	—
Agrostis stolonifera . . .	—	40	80	—
Atriplex Babingtonii . . .	20	—	—	—
Carex arenarea	—	40	60	100
Festuca rubra	—	40	60	20
Psamma arenarea	—	60	80	100
Crambe maritima	—	—	20	—
Rumex crispus	—	20	20	—
Taraxacum officinalis . . .	—	—	20	60
Sedum maximum	—	—	40	40
Viola tricolor	—	—	20	60
Anthoxantum odoratum . . .	—	—	—	20
Galium verum	—	—	—	60
Heiracium umbellatum . . .	—	—	—	40
H. pilosella	—	—	—	40
Rumex acetosella	—	—	—	80
Veronica officinalis. . . .	—	—	—	20

Similar zonation is always found where the source of water lies at one side of the habitat, on the edge of lakes and rivers, on bogs and moors.

Humidity, wind, and insolation—all factors which influence transpiration—differ markedly over quite restricted areas, and give rise, therefore, to local differences in the "transpiration climate" (Stocker, 1923; Vallin, 1925; Walter, 1928).

An interesting situation occurs in bogs and moors where the water covers the vegetation for part of the time. There arises a competition between mesophilous and hygrophilous plants. (*See* p. 117, and Vallin, 1925.) The smallest elevation of the level of the soil alters the humidity relationships, and the vegetation as a consequence is very varied. Such mixed formations, which repeat on a small scale the competition between the plant geographical formations, amply repay ecological study.

CHAPTER V

THE ECOLOGICAL PROPERTIES OF THE SOIL

FROM the standpoint of ecology, the soil might be defined as that part of the earth's crust which bears plant life. According to this definition, the solid rock covered with lichens is as much soil as forest humus, or mud in still pools. Even in a completely inorganic soil, a characteristic exchange of material goes on between soil and plant; for it is from the soil that the plant obtains part of its food, the cations and anions essential for life, together with a number of less important materials.

Under exceptional circumstances the sub-aerial parts of certain plants may absorb nutrients dissolved in the rain, such as ammonia, directly. Sphagna on a moor must obtain their mineral matter from the air; and adaptations of epiphytes in this direction are described by Haberlandt (1921). Wetzel has shown, more recently, that the absorption of water by the subaerial parts of most plants is of no ecological significance (1924). There is in the higher plants, at any rate, a fairly sharp distinction between nutrition from the soil and from the atmosphere. Even rooted water plants obtain a part of their inorganic nutrient from the soil, although their leaves are surrounded by a culture solution. Pearsall has found (1920) that the soil in the English lakes exerts an indubitable influence upon the zonation of the vegetation.

That this anatomical and morphological separation of the means of salt uptake and the carbon dioxide intake has not occurred by simple steps in phylogeny, needs no further explanation here. The differences in structure between root and shoot, so clearly described by Sachs (1887), need only be touched upon briefly.

It is of primary importance for both absorptive organs, leaf and root, to have a large surface. Other conditions being constant, the rate of uptake is proportional to the area of the surface. For the leaves a large flat surface is necessary, in

order to intercept as much of the light as possible.   Often, too, this is of advantage for the uptake of carbon dioxide, for a flat horizontal surface will absorb carbon dioxide from the air above and that rising from the soil below.

The chief necessity for the root is the development of a very large absorptive surface, and this is attained by repeated branching and by the formation of root hairs.   The root also serves to anchor the plant in the ground; and this is effected by the formation of lignified mechanical tissue.   Another characteristic of the root is the continued growth of the root tips, which are always exploring new ground.   The root hairs, which are very intimately associated with the soil particles, are very short-lived; this may have some significance, for the acids which are given off by exosmosis from the dead root hairs, will facilitate the chemical decomposition of the soil.   Moreover, in the organic remains bacteria breed, and these are useful in the manufacture of suitable nutrients.

Just as light is the determining factor in the formation of the aerial absorptive organs, so the formation of the roots is governed principally by water, although some influence is exerted by the chemical composition of the soil, and the nature of the "soil atmosphere."

With a low water content the root system is only weakly developed.   As the water content is raised the size of the root system becomes bigger, and the amount of branching, and the number of root hairs, is also increased.   If the water content is raised beyond its optimum value, the growth of the roots, and their branching, become progressively less and less.   This is probably due to insufficient aeration of the soil.   It is known that a high carbon dioxide concentration of the soil, which is a consequence of bad aeration, has an inhibitory effect upon the growth of the roots.

On the chemical side, the action of phosphates, nitrates and calcium ions has been closely investigated.   Phosphates promote the growth of roots, and particularly a very rich branching, so that a thick network is formed (Tottingham, 1914).   Calcium, too, in moderate concentrations, stimulates root branching, and in the soil seems to favour growth in length, though in water cultures growth in length seems to be inhibited (Hansteen-Cranner, 1910; Lundegårdh, 1911). According to Maquenne and Demoussey (1917; 1919), the development of the roots of pea seedlings stops in three or four days in the absence of calcium, the calcium stored in the seed

M

being sufficient for growth. As a rule, the presence of nutrient salts in the soil furthers the growth of the root system, although certain exceptions do occur, about which no generalization can be made. It has been observed, for example, that a lack of nitrogen in the soil promotes the growth of roots (Benecke, 1903; Brenchley and Jackson, 1921; Turner, 1922).

The outcome of this interrelationship between the constitution of the soil and the development of the root system has naturally a great effect upon the uptake of salts by the plant, and this in turn reacts upon the formation of the aerial parts. A difference in the development of the leaf area, or the amount of chlorophyll, or the amount of branching, will cause a difference in the intensity of assimilation, which will affect the activity of the whole plant. By reason of this complex chain system of the formative processes, an apparently insignificant change in the structure of the soil can determine the prosperity of a plant, and even its geographical distribution.

In this connection reference must be made to the interesting deduction of V. H. Blackman (1919) on the applicability of the compound interest formula in plant physiology.

In the formula:

$$W_1 = W_o\, e^{rt}$$

W_1 is the weight of the plant after time t, W_o the weight of the seed, t the time for which the plant has been growing, and r the "efficiency index." Blackman found that in some experiments of Gessler (1907), upon *Helianthus*, r remained approximately constant until the time of flowering, and then its value sank. It follows from the formula that a high yield of organic substance will depend upon a high weight of the seed, and a high value of r. Moreover, a very small increase in the efficiency index, operating over a long period, can result in a very big increase of the yield. Blackman calculated that an increase of 6 per cent in the intensity of assimilation would result after 100 days in an increase of 50 per cent in the dry weight. A close observation of the relationship indicated by Blackman, and its positive proof, would be of particular value in practical plant culture.

In their ecological effects, many of the atmospheric factors are dependent in some way or other upon the soil. The temperature factor, for instance, acts principally through the soil temperature, which in its turn depends upon the heat absorption and the capacity for heat of the soil. The supply

of carbon dioxide, too, depends to some extent upon the micro-organisms in the soil, and the principal action of rainfall is that it regulates the water content of the soil. In fact the only factor which may be said to act independently of the soil is the radiation from the sun. In the following pages the influence of the soil upon plant growth will be considered in more detail.

1. Development of the Soil

In nature the simplest substratum for supporting life is the naked rock. Under these conditions, the water supply, which, as we have seen, is the most important factor in vegetation, is uncertain and fortuitous, so that lithophytes are small, slowly growing plants, capable of withstanding periodic desiccation; algæ and lichens. The composition of a rock vegetation is dependent upon all those factors which influence the water supply, i.e. the exposure, slope to the horizontal, and so on; and also upon the intensity of weathering, and the supply of nutrient materials (see Sernander, 1912; and Nienburg, 1919). A rock "prepared" by *Cyanophyceae* and crustaceous lichens can gradually be colonized by mosses and bigger lichens, followed by certain unassuming phanerogams. At this stage a certain amount of humus has been formed, so that the water balance is much better. Where clefts in the rock occur in which humus can be accumulated, chasmophytes are to be found (Plate VII).

This process, the building up of a soil, can be observed anywhere that naked rock is to be found. All processes which tend to break up the rock—weathering, frost, temperature changes, etc.—accelerate the formation of the soil. In the later stages of the process their action is replaced by the chemical action of the plants themselves. The solvent action of the carbon dioxide given out by the roots and rhizomes, and that of the organic acids which are eventually formed, is assisted by the acid humus material, and at this stage begins that phase of soil development which is of such importance for the prosperity of the more pretentious higher plants.

The pulverization and the distribution of the mineral constituents of the soil are influenced by a number of geological processes. Flowing water, glaciers, and wind carry the soil from one place to another, and deposit it in new regions.

The rain which trickles through the soil carries down with it the finer constituents. It is for this reason that the slopes of mountains are poor in the finer soil particles, which are carried

into the valleys or into the plains below. A considerable proportion of this fine, floated matter reaches the rivers; it is then spread over the neighbouring fields when floods occur, or it reaches lakes or the sea and is there precipitated. River floods in Northern Europe and America are for this reason of considerable significance in the formation of soils.

The co-operation of plants in the building up of the soil can be seen everywhere along the sea coast. In creeks and still inlets there is a continuous building up of the soil, where the sand and mud brought up by the currents are slowly laid down (Walter, 1927, has given a detailed description of the northern coast of Germany).

Such a deposition of new soil on the northern coasts, where the ebb and flow is not of any importance, is materially accelerated by *Zostera marina*, whose creeping rhizomes bind the sand, and between the tufts of whose leaves the newly deposited sediment is firmly held. As the level of the deposits becomes higher, *Zostera* grows outwards, until the ground is raised so high that it is from time to time laid dry. Then other plants colonize the deposits, *Salicornia herbacea*, *Spergularia salina*, *Glyceria maritima*, etc.; plants which are able to endure periodic submergence under the water. The thick turf of *Glyceria*, *Triglochin*, *Juncus Gerardi*, and other turf-building herbs spreads horizontally, and finally knits together, to form a continuous layer of vegetation. Since the soil level, when it reaches this height, is not built up any higher, there persists a continued struggle, which can be followed from year to year, between the sea and the sand-binding plants. Such a layer of vegetation is sometimes destroyed by continued high water in storms, or by the formation of ice in winter.

The new soil formed at the edge of glaciers in Western Alaska has been studied by W. S. Cooper (1923). The earliest plant inhabitants are xerophytic mosses, small herbs, *Epilobium*, *Saxifraga*, *Dryas*, and dwarf willows (*Salix arctica*). Gradually willow and alder bushes appear, and Sitka-spruce, and this, in the course of time, leads to coniferous forest. On the rocks, colonization of the cracks takes place, exactly as in similar habitats by the sea. The colonization on blocks of rock, broken stones and pools, never proceeds beyond the "pioneer" stage (*see* Walton, 1921, on succession in Spitzbergen).

The colonization of loess is to some extent reminiscent of that described above in the formation of land from water deposits. Loess is a very fine soil deposited by the wind. A

PLATE VII

(a) Vegetation of *Armeria elongata*, *Plantago maritima*, and *Glyceria maritima* in the cracks of an almost horizontal rocky shore of Cambrian sandstone at Cattegat.
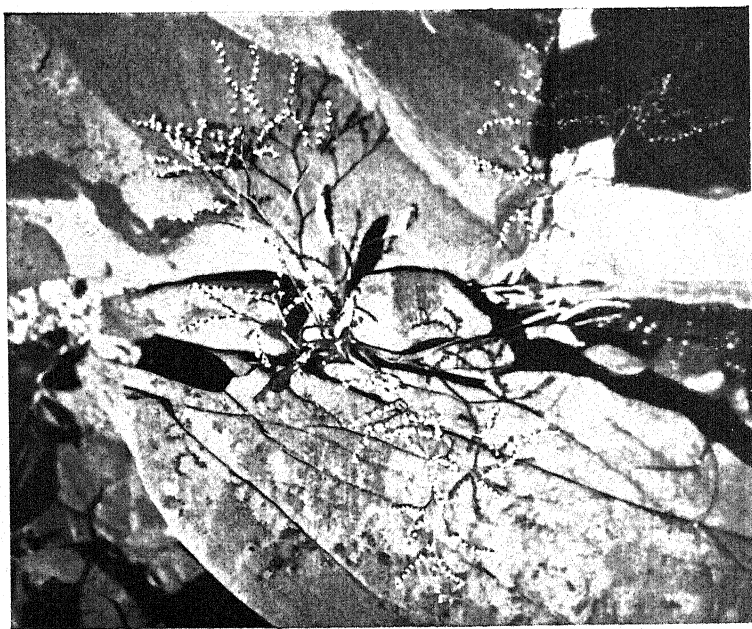
(b) *Statice bahusiensis*, a typical chasmophyte in the lower supra-litoral zone.

great part of Asia, Eastern Europe, and North America is covered with such deposits, and these areas are mostly occupied by the characteristic vegetation of steppes or prairies.

The sand was originally colonized by the same types as colonize the dunes, principally xeromorphic grasses, herbs with creeping rhizomes, which rise higher as newer layers of sand are deposited. The plant pioneers are represented by *Carex arenaria*, *Hordeum arenarium*, *Psamma arenaria*, *Elymus arenaria*, *Tritilum junceum*, *Honckenya peploides*, etc. After these pioneers have bound the sand, other plants can establish themselves (Yoshii, 1919; Braun-Blanquet and Marie, 1924). Between the pioneers and the closed formation which is the climax, there is a definite succession, and a concomitant change in the water economy of the soil. The climax formation of sand soils can be grassland, *Calluna* moor, or forest, according to the situation. As a rule, the deciding factor is that of water, especially the relation between evaporation and rainfall.

The course of development of the vegetation in sandy soils is very similar in different climates, though the actual species participating in the succession may vary according to the region. The pioneers of sandy areas and dunes are extreme "competition forms," adapted to the movement of the sand and the inadequate water supply. Where the water balance is favourable the pioneer plants are replaced by mesophytic successors. This process of succession is accompanied by a development of the soil and a formation of humus. The root system and the rhizomes are of great significance in the colonization and building up of the soil. It cannot be too strongly emphasized that the soil is the product of an interaction between the plant itself, the available geological material, and the various geological and climatological processes. This fact is sufficient to explain the stability of many plant societies, and their relative independence of the constitution of the underlying rock; it throws light, too, upon the order of succession in ecology. As another example of the co-operation of plants in the formation of the soil may be mentioned the mode of colonization of fresh water deposits. On the sea shore, only halophytic plants can enter as pioneers, but around fresh-water lakes a number of hygrophytic types can establish themselves, and in the shores of lakes and bogs there is a very definite succession. From the luxuriant growth of *Scirpus lacustris* and *Phragmites communis* are derived large

quantities of dead material which, together with mineral matter, form new soil. In this way the soil level is gradually raised, and shore plants, such as *Sparganium, Carex, Lythrum salicaria*, and others, gradually spread toward the water's edge. Eventually a moor, with species of *Carex* and *Agrostis*, will succeed to the ground, or, under favourable conditions, it may become covered by forest. If *Sphagnum* enters in the early stages, a deep moorland soil will be formed, which can ultimately be covered by woody plants or by *Calluna* and *Vaccinium*.

The quantity of food material in a soil depends naturally to some extent upon its physical and petrographical constitution. No amount of weathering will produce nutritive materials from a soil of quartz sand. But where the soil is of such a constitution that it will yield soluble materials upon weathering, then the availability of these materials for the plant will depend upon the type and intensity of the weathering which the soil undergoes. And in this process the climate, especially the temperature and the rain, plays a prominent part.

The relation between the rainfall and the evaporation is the deciding factor as to whether the products of weathering remain in the soil, or whether they are carried through the soil. In a damp climate the annual rainfall is greater than the evaporation. The surplus water as it flows away, carries the salts into the rivers, and thence into the sea, and it is because of this that such a rich flora can develop in the waters; but this removal of salts from a damp soil leads eventually to a condition unsuitable for plant growth. There is a continual leaching out of mineral salts. Especially in the colder zones, where the rate of weathering and decomposition is slower, rich desposits of humus are to be found, and there is a tendency toward the development of acid humus. The "podsols" of the coastal regions of Europe, and the "brown earths" of Central Europe, are examples of such damp soils.

In regions where the soil is dry, evaporation is in excess of rainfall, and, as a result of this, the products of weathering accumulate in the soil. Under such conditions raw humus and moors are seldom formed, even when the decomposition is inhibited. While, however, an arid soil is amply provided with nutrient salts, vegetation is often limited by the water factor. When sufficient water is present, these arid soils are the most fruitful of all; and it is no coincidence that the original cultures of the human race developed upon such soils

as these (Hilgard, 1906; Gradmann, 1906; Vahl, 1911; Köppen, 1923, p. 102; Whitney, 1925).

In the neighbourhood of climatic boundaries there are naturally transitions between humid and arid soils. Under a rainfall of about 100 mm. a soil can develop in one direction or the other (Lang, 1920). The "evolution" of a soil is a process which can never be regarded as quite completed, for sometimes the climate changes gradually, and sometimes the plants themselves influence the soil. It is an evolution which extends over long periods of time, and therefore it cannot be followed directly. The mode of origin of many soils is quite unknown, while that of others is the subject of a great deal of discussion; and even where the problem has been critically studied, the conclusions as to the evolution of the soil depend upon comparisons and are supported by hypothetical assumptions.

Obviously the genesis of soils, from the standpoint of the ecologist, is of less interest than their present constitution; and this can be determined with more or less accuracy, so far as our present and somewhat inadequate methods of analysis go. The present discussion will be confined to a few typical soils, and reference will be made to the pertinent books on soil science.

2. "PODSOLS"

These soils are particularly characteristic of the coast climate of Europe (Fig. 56). The "podsol"[1] has been chosen as a type; it has been described by Wiegner (1921) as an extremely damp soil. It has a wide distribution over Europe and occurs on the coast-line in Western and Central Europe, where conditions are distinctly moist on account of a high rainfall and low evaporation. Toward the north-east its area widens, since the low temperature in Scandinavia and Northern Russia lowers the evaporation, and also by its own action increases the salt content of the soil. (On the subject of distribution of podsols, see Müller, 1887; Glinka, 1914; and Lang, 1915.) Ramann has divided the podsols into five different groups, which for the most part occur along the coast-lines: the Atlantic group, those of Western Germany, Northern Scandinavia, Northern Russia, and German-Russia. Common to all these is a definite stratification, where the humus directly overlies the mineral soil beneath;

[1] The name "podsol" is derived from the Russian. It has been retained by Marbut and Shantz untranslated.—*Vegetation and Soils of Africa*, 1923.

A. Humid Region
- Mountains
- Tundra
- Atlantic Coast
- N.Germ. & Scandinavian
- Moors
- N. Russia
- Brown Earths
- Red   ,,

B. Arid Region
1. With Cold Winter
- Black Earths
- Salt Soils
2 With Warm Winter
- Spanish Steppes
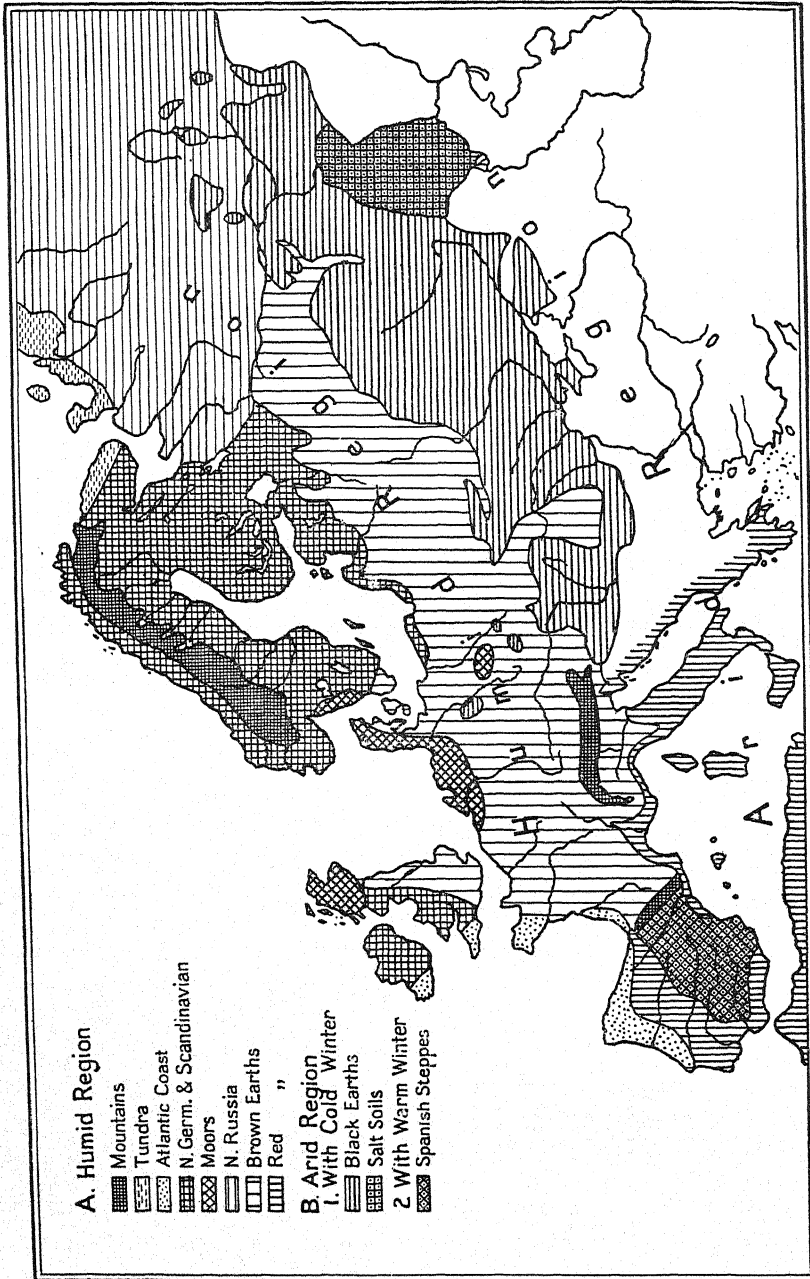
FIG. 56.—Soil Map of Europe. (After Ramann, 1911.)

the upper layers of the mineral soil being markedly leached out.   This removal of soluble materials, inclusive of iron and phosphoric acid, is the result of the action of an absorptive unsaturated humus material, and varies according to the climate.   The water table in such soils is generally high.

The northern coniferous forests grow almost exclusively upon soils of the "podsol" type (Tamm, 1920; 1921).   The process of the formation of podsols has recently been very thoroughly investigated by Hesselmann in Sweden (1926) and Weiss in Denmark (1929).   On account of the humid and cold climate, the decomposition of humus proceeds slowly, and those forms of vegetation are favoured which produce a thick, tough type of humus.   The remains of vegetation, straw, etc., incorporated into the soil, are only gradually attacked by bacteria and fungi; so that the humus consists of a half-destroyed mass, in which the structure of the organic remains can still be distinguished.   This acid humus lies as a well-defined layer over the mineral soil beneath.   Similar turf-like layers of humus may be formed in more open habitats, for instance, on moors of *Calluna* and *Vaccinium*.

The term humus embraces an immense number of organic compounds (Russell, 1927, p. 197) which have this property in common, namely, that they have arisen from carbohydrates, mostly cellulose.   Nitrogen is present only from "pollutions" (Detmer).   The chemical composition of humus is far from understood, and of more immediate importance is the fact that the humus materials all occur as colloids, in degrees of dispersion changing according to the prevailing conditions.   Stress has been laid upon the fact by Waksman (1926; 1927) and other workers, that in "finished" humus the ratio of carbon to nitrogen is almost constant, from 8/1 to 12/1.

It is well known in colloid chemistry that the degree of dispersion depends to a great measure upon the electrolytes present.   The disperse phase always carries an electric charge, which is generally negative; this charge, in fact, is the pre-requisite of the disperse phase, for the charged particles repel one another.   Bases in the colloidal condition, aluminium and iron hydroxide, for instance, carry a positive charge.   If an electrolyte, such as potassium chloride, is added to a highly dispersed colloid, the charged ions act upon the charged colloidal particles in such a manner that the colloidal particles lose some of their charge, and flocculate into bigger particles.

Half-decayed humus material is, from the beginning, in a very high state of dispersal. In the upper layers of a podsol there is a great shortage of salts; moreover the highly dispersed organic material is less sensitive to flocculation by electrolytes than the inorganic colloids of the soil, so that the humus colloids remain "unsaturated" ("absorptiv ungesättigt"), since their large inner surfaces retain great potentialities for adsorbing material. They have an acid reaction, since the cations in them are absorbed from a neutral solution: in fact, they are regarded by many chemists as acids. The mode of origin and the development of this "unsaturated" layer of humus is by no means fully understood. The nature of both the fauna and the flora of the soil is of importance. In the absence of earthworms, for instance, the intimate mixing of humus and mineral particles does not occur. Fungal hyphae bind together the soil and hinder the aeration; this in turn slows down the rate of decomposition. In a coniferous forest, for example, the degree of podsol formation varies with different types of soil vegetation (Tamm, 1920). The *Myrtillus* type of ground vegetation facilitates humus formation most, and next to this comes the *Vaccinium* type. The lichens are the most feeble in their influence upon humus formation. A ground vegetation of *Oxalis* and *Maianthemum* results in an incomplete formation of podsol; it would seem that the formation of humus from plant remains is more difficult from some plants than from others. Hesselmann's work (1926) has shown that the acid or basic buffer content of the layer of decayed vegetation is of importance in the formation of podsols. Hesselmann distinguishes five different types of decaying vegetation:

(1) That with a high acid and a low basic content in buffer substances. To this class belong the plant remains from northern coniferous forests, from Junipers, from dwarf shrubs such as *Calluna* and *Empetrum*, and from *Hylocomium*.

(2) That with a moderate content of acid, and a fairly high content of basic buffer substances; a type to which most deciduous trees belong, and a number of herbs characteristic of coniferous forest.

(3) That with a very low content of acid and a high content of basic buffer substances. To this group belong the vegetable remains of hazel, elm, and of *Stachys sylvatica*.

(4) That with a high content of both acid and basic buffer substances. This is a heterogeneous group to which belong maple, oak, larch and *Geranium sylvaticum*.

Finally (5) that with a very low concentration of buffer substances, for example, the grass *Deschampsia flexuosa*.

It is clear, then, that although the content of buffer substances may depend to some extent upon the structure of the soil beneath, yet the buffer value of the decaying vegetation is specific to the species of plant.

Moreover the level of the water table and its movements affect the formation of humus. A local difference in the water may determine the development in one direction or another. Hesselmann (1910) shows how water rich in oxygen promotes the growth of a mesophilous vegetation, with the consequent formation of a "mull" soil; and Glinka (1914) has described how podsols are formed, especially in valleys, on plains and on plateaux, rather than on the slopes of hills. Nor must the climate, in that it affects the speed of chemical and biological processes, be left out of account.

Some of the acid humus materials are soluble in water, and these are regarded by some authors as the humic acids (Huminsäuren; Odén, 1919; Russell, 1927, p. 168). As sols, these are comparatively insensitive to electrolytes. They act—and this is of particular importance—as protective colloids, i.e. they prevent or retard a number of ion reactions (reaction of ferric ion with potassium ferrocyanide) and the mutual precipitation of colloids with opposite charges, such as silicic acid sol and aluminium hydroxide.

On account of this protective action of the acid humus sol, the end stages of weathering in the mineral soil under a layer of humus proceed in a manner quite different from that which obtains when the humus is not present. In chemical weathering, which may be broadly considered as a hydrolysis (Ramann, 1911; Wiegner, 1921), the alkali ions are liberated as hydroxide, the alkali earths and iron, in the presence of sufficient carbon dioxide, as acid carbonate, go into solution as their respective hydroxysols; (the solution of iron is accelerated by humic acids (Ehrenberg, 1918)) and aluminium hydroxide and the hydroxy silicic acids appear as colloidal gels and sols. Beside these there occur all sorts of intermediary chemical and adsorptive compounds. In the absence of protective colloids the number of these adsorptive compounds is rather large. Especially common is a combination of the aluminium hydroxide sol and silicic acid, to form the so-called exchange zeolites, which are the main constituent of clay. The clay remains at the end of the process as an insoluble product, and

contributes markedly to the fertility of the soil. But if a protective colloid, such as a humus sol, is present, the mutual precipitation of the aluminium hydroxide and silicic acid sols is prevented; they remain in solution and are carried away by the ground water. In this way the so-called "bleached sand" is formed. In precisely the same way iron hydroxide can disappear entirely from the weathered surface of the soil, depriving it completely of colour.

In the course of time such an impoverished soil is reduced to between 10 and 20 per cent of its original weight (Tamm, 1920). Some of the dissolved substances, especially the iron and the silicic acids, are precipitated again in the layer of soil underneath the impoverished soil, and in consequence, this layer attains a brown-red colour. The aluminium hydroxide is also partly precipitated. In this way there is formed beneath the surface a hard "pan" of precipitated colloids, humus, iron hydroxide, aluminium hydroxide, and silicic acid. These cement the sand particles together.

Various views have been put forward as to the cause of this precipitation of iron and silicic acid in a certain zone. Ramann (1911) assumes that there is less weathering in the lower than in the upper layers of the impoverished soil; this is accompanied by an increase in the concentration of the salts, and a consequent precipitation of humates. According to another hypothesis, put forward by Morison and Sothers (1914), the increase in concentration takes place in summer, when the soil is partially dry; the level of the water table sinks, and the colloidal materials accumulated during the winter are precipitated. The accumulation of materials in the sub-soil of a humus soil, can be very considerable (Table XXIX; and *see* numerous analyses by Tamm, 1920).

Materials which are not precipitated in the sub-soil disappear with the ground water to form the mineral constituents of water in rivers and lakes. Sodium, potassium, calcium, magnesium, and iron, reckoned as oxides, are present to the extent of one part per hundred thousand in the Swedish rivers (Hofman-Bang, 1905); and according to the calculations of Tamm (1920) the same amounts are present in the water draining through the podsols of Swedish forests. Pearsall (1920) has made similar observations upon the mineral content of English lakes. So the salts washed out of a podsol may still benefit plant life in some other place.

It is to be observed from Table XXIX that the more

TABLE XXIX

WEATHERING AND PRECIPITATION IN HUMUS SOILS
(Morison and Sothers, 1914.)

	Bleached Sand.	Pan.	Soil below Sand.
Loss on ignition . . .	1·84	7·22	1·36
Fe$_2$O$_3$	} 0·493	4·066	3·211
Al$_2$O$_3$			
CaO	0·080	0·350	0·106
MgO	0·063	0·084	0·110
K$_2$O	0·087	0·155	0·152
P$_2$O$_5$	traces	0·037	0·018

useful salts of the alkalis and alkali earths are precipitated to a smaller degree than the less important compounds of iron and aluminium. Moreover it is often impossible for roots to penetrate the pan beneath the soil surface. (*See* Warming-Gräbner, 1915–18, and Tamm, 1920.) The materials accumulated in the pan are therefore not at the disposal of the plant. This is of importance in the ecological relationships of podsols, a subject which must now receive some consideration.

There are three peculiarities of podsols which are important for the composition of the vegetation growing upon them:

1. The washing away of nutrient materials from the neighbourhood of the roots, into the soil beneath.

2. The prevailingly high hydrogen ion concentration.

3. The frequently inadequate aeration, which is aggravated by the high water content.

The poverty of nutrient materials excludes the more pretentious plants, especially herbs, which extract their nourishment from the superficial layers of the soil, where the salt concentration is low. The dominant vegetation, therefore, consists of "oligotrophytes," perennial grasses or herbs with rhizomes (*Aira flexuosa, Festuca ovina, Molinia coerulea, Pirola, Monotropa, Maianthemum,* etc.), numerous mosses (*Hylocomium, Polytrichum,* etc.) and dwarf shrubs (*Calluna, Vaccinium, Empetrum,* etc., and in the North, *Betula nana, Salix,* and others); and in dry situations, various lichens. This thick vegetation itself has a secondary effect upon the composition of the soil; and prepares it, as it were, for even more extreme formations.

The mosses with their wefts of rhizoids, and the richly branched and threadlike roots of *Calluna vulgaris* and *Vaccinium myrtillus* contribute markedly to the formation of a thick impervious layer of humus. The roots scarcely penetrate at all into the mineral soil beneath, especially if the stand of plants is close. This matting of the humus is increased, especially in woods, by the numerous fungal *mycelia* present; while bacterial activity is restricted owing to the high hydrogen ion concentration, and to the periodic desiccation. Very often the whole layer of humus can be torn up as a compact mat from the mineral substratum.

This mat of humus prevents, purely mechanically, the penetration of the roots of certain plants. Moreover the more sensitive plants are suffocated, on account of the bad aeration and the excess of carbon dioxide. Some plants typical of podsols, such as the dwarf willows in the north, can live in a soil which is almost free of oxygen (Clements, 1920; Romell, 1922; Lundegårdh, 1924, Chap. V). The work of Romell (1922) has shown that the poor aeration of humus soils has been somewhat exaggerated. Noticeable lack of oxygen at depths between 10 and 20 centimetres is rarely to be observed. Only when the drainage of the soil is inadequate, as in some boggy soils in coniferous forests, does the oxygen content fall to 1 per cent or less.

The appearance of the humus varies according to the dominant plant growing in it. The humus under bilberries is loosely compacted, a condition which can be traced to the numerous creeping stems; that under whortleberries is thicker, while humus under heather is black, thick, and impermeable to water. This impermeability of raw humus, and the ease with which the upper part will dry out, prevents indirectly the evaporation of water from the deeper layers; and for this reason an acid humus soil is liable to become boggy. In the following table the pore volumes of three types of humus are given:

<div align="center">

TABLE XXX

(Figures from Ramann.)

</div>

		Pore Vol.
Soil under beeches	. . . . .	59·48 per cent.
„ . bilberries	53·33 „
„ mosses and dry grasses	. . 49·55 „

Boggy podsols of this type are found in the spruce forests of Northern Sweden. In these instances a contributory factor

is the formation of pans, which prevent the flowing away of water and hinder the production of deep-seated roots of trees. The pines and spruce growing on pan soils are obliged to develop superficial roots, spread out over the surface of the pan.   It is evident that, for this reason alone, humus soils are unsuitable for the growth of trees, and that the conditions are still less suitable when pans are formed; forests growing upon such soils in Denmark and Northern Germany are somewhat weakly, though in Sweden (Tamm, 1920) the conditions are somewhat better.   The less pretentious conifers, pines and spruce, are the most widespread, and, where they do colonize ground, they tend to inhibit the formation of dry peat or raw humus.   According to Ramann (1911, p. 209), the spruce is able to endure the unsuitable dry peat more easily than any other of our trees; and while it is driven out of more favourable habitats by the competition of other species, it succeeds on peat, where other species cannot compete with it.

Three causes contribute to the formation of peat in spruce forests: first of all there is a close, thick layer of needles, which is bound together by numerous wefts of fungal hyphae; secondly, there is the form of the branches, which allow the rain to run off quickly, and bring about a silting up of the soil; lastly, there are the roots, which branch finely, and run horizontally, forming a tough turf which decays with difficulty. This consolidation of the soil is in itself inhibitory to the spread of the very species growing in it.   It is for this reason Gräbner (1918) considers that the roots of every generation of spruce are more superficial than those of the preceding generation.

Deciduous temperate forest is rarely found on a raw humus soil, though such a "facies" is known to occur. Warming (1909) has described a beech wood on raw humus soil in the following terms:

"The soil is usually firm, and penetrated by roots and mycelium, and the pore volume has been reduced.   There are no earth-worms, and the soil is not aerated so that humic acids are formed; it is often dried out by the sun, and the covering of leaves is often blown away.   On such a soil there thrives a thick vegetation of *Aira flexuosa*, a fine-leaved and xerophilous grass, *Trientalis europea* (typical of raw humus), (Müller, 1878–84), *Maianthemum bifolium*, etc., and a rich carpet of mosses: *Polytrichum*, species of *Hypnum*, *Hylocomium*, *Dicranum*, *Leucobryum*, species of *Mnium*, and even isolated *Sphagna*.   *Calluna* and *Vaccinium myrtillus* often appear, and

then the ground approaches a 'Calluna moor.' When development of the soil takes this course, the conditions often become unsuitable for beechwood, and it disappears, leaving often a Calluna moor in its place."

In oak woods this tendency to develop a raw humus soil is much more rare, since the dead leaves from oaks are much more easily decomposed, and since the oak roots break up the soil to a much higher degree than the roots of beech. Generally speaking, the formation of podsols in deciduous woods takes place more commonly along the climatic boundaries. The beech woods in Western Scandinavia, for instance, under the influence of the coast climate, take this course of development, and the same course is taken in Northern Germany, while in South-east Sweden the formation of podsols is less common.

Up to the present, attention has been confined to the climatic and biological conditions for the formation of podsols. It is a remarkable fact that the petrographic character of the sub-soil has a relatively small influence upon the formation of the soil itself. There is no doubt, however, that in the early stages the lime content is a deciding factor. The calcium ion has a marked ability to flocculate the humus sols, and this in turn promotes the breaking up of the soil; and when there is sufficient calcium in the humus layer, a raw humus soil is not produced. However, rain-water, charged with the carbonic acid produced by decomposition, trickles through the soil, and gradually dissolves the lime out of the upper layers; and it is either precipitated at deeper levels, or lost altogether. As soon as the formation of raw humus has begun, the fauna characteristic of a real mull soil disappears; and the presence of this fauna is essential for the mixing of the upper layers of humus and mineral matter underneath. The development of a soil toward raw humus can well be considered as a chain of interlocking processes which in their turn depend upon other conditions, such as the climate and the composition of the flora.

Just as the raw humus soil is the outcome of a development guided by climatic, edaphic, and biotic factors, bound up with a definite succession of the vegetation, so it can be said that every raw humus soil is the starting-point for some further course of development. Strictly speaking, the evolution of such a soil is never quite at an end, since the climate is always undergoing gradual change, or temporary fluctuation. But the general direction of such a development can usually be determined, and certain climaxes (in Clements' sense of the

word, 1905, 1916) can be recognized; periods when the development remains stationary for some time, before beginning to change again. Podsols provide good examples of this gradual metamorphosis of soils.

Brief mention has been made of the formation of bogs in the coniferous forests of the North. This phenomenon has been described by a great many investigators, without any clear statement having been made as to the causes of the development. One thing is clear, namely, that *Sphagnum*, once it has appeared, is an active agent in raising the level of the water table. As the process of forming the bog proceeds, the former woodland plants die out; and finally the trees, which cannot endure a sodden soil almost free of oxygen, disappear (Hesselmann, 1910). In the next stage, other extreme hygrophytes, beside *Sphagnum*, enter the habitat, plants which can endure high hydrogen ion concentration and whose roots need very little oxygen: *Carex globularis, Equisetum globularis, Eriophorum vaginatum, Rubus chamaemorus, Myrtillus nigra* and *M. uliginosa, Ledum palustre,* etc.

Another type of development occurs in woods with very pervious acid soils when, for some reason or other, the reproduction of the trees is not continued. The soil dries out and is occupied by heather and bilberry. Gradually the wood is transformed into a heath. Gräbner (1895) and Ramann (1911) consider the formation of heath as an evolution proceeding "backwards" of its own accord, a retrogression. Clements, on the other hand (1916), regards the forest as the climax, and considers that the heath is only one of the earlier stages of development, reproduced by the peculiar conditions prevailing.

The contrast is, however, only a matter of nomenclature. There is no doubt that though the wood is a stable formation, it must give way to other formations if the climate conditions alter. In the absence of any direct experimental evidence the whole matter must be left open.

It will be well to summarize briefly the development of raw humus soils.

The early stages of development are naturally more or less the same for all soils. Through the action of the pioneer plants there is deposited a thin covering of humus over the soil beneath, which soil may consist of rock, diluvium or alluvium. The geological constitution of the sub-soil generally plays some part in the later stages of development, to this

extent: that soils which weather easily, or which yield large quantities of plant nutrients, tend to form a layer of humus which is neutral and "saturated." The buffer action of the decaying vegetation must always be taken into consideration, though, under certain circumstances, it may be neutralized by the action of the soil.

Two types of evolution of raw humus soil can be distinguished. In the first type, as the humus layer increases in thickness, there occurs, in a humid climate, an ever-increasing leaching out of the upper layers (quantitatively estimated by Miller, 1918). The humus becomes transformed into a highly dispersed form, and, as an acid sol, goes partly into solution, and begins its action upon the weathering layer of the mineral beneath.

Under these conditions the weathering does not yield zeolites (clay), and the hydroxides of the alkali metals are very little adsorbed. Everything which is dissolved out (i.e. alkali hydroxides, aluminium oxyhydrosols, silicic acid hydrosols, colloidal iron hydroxide, etc.) is carried to the sub-soil, and there partly precipitated, to form pans. The upper layers of the soil, in which the roots develop, become poorer and poorer in nutritive materials, and this creates a tendency for the vegetation to become more oligotrophic.

When the evaporation is cut down, the water content of the soil becomes greater, especially if it is covered by forests; the natural drainage of the soil is inhibited by the pan beneath, and a process of bog formation begins. *Sphagnum* appears, and the level of the water table becomes higher. It is this process which gives rise to a moor with its sparse vegetation of bog plants specially adapted to a badly aerated soil. The water, which lies almost on the surface, is chemically altered by the *Sphagnum* (though the mechanism of this change is not understood), and this in its turn leads to a still greater specialization of the moorland vegetation.

The second type of humus development leads to a heath formation, in which the level of the water table is lower, and therefore *Sphagnum* cannot take hold upon the soil. The growth of woodland is inhibited more and more by the pans which form, and the soil becomes more and more shallow. Woody plants, such as *Calluna*, *Vaccinium*, and the dwarf willows, which can endure periodic desiccation, are the dominant plants.

The low level of decomposition of the humus has been

suggested as one of the causes of the formation of podsols. This would mean that with decrease of temperature, the assimilation of carbon dioxide decreases more slowly than the activity of bacteria and fungi, which latter follow the growth curve described on page 75. It may be that the growth of some micro-organisms is decreased more than others by the same drop in temperature, and this might too change the source of decomposition of the humus soil. No work seems to have been published upon this important question. The action of temperature in the formation of podsols is of the first import-ance, but temperature alone will not account for all the pheno-mena of the process; other factors beside a damp and cold climate must be taken into account.

In the tropics, so far as is known, the formation of podsols is somewhat exceptional. Decomposition proceeds very rapidly, more rapidly than the formation of new organic material. As a rule, a layer of humus is not formed at all; as quickly as dead organic material is destroyed, it is incorporated into the soil. Weathering in the tropics, too, is a far more rapid process, and proceeds in directions different from those followed in temperate regions. An accumulation of alumi-nium and iron hydroxides takes place, giving the soil a red colour. According to Lang, red laterite is formed if the temperature of the soil is above 20° C.; between 15° and 20° red earths are formed, and below 15° C. yellow earths. The last two soils are found in the Mediterranean region.

Most widespread in Central Europe are the brown earths. They form the normal substratum of deciduous forests. The humus is not stratified, but mixed intimately with the mineral particles; it is also more nearly neutral than are the podsols. The petrographic constitution of the underlying rocks plays a greater part here than it does among the podsols. The most important constituents of the brown earths are the exchange zeolites, the formation of which has already been discussed. On account of the neutrality of the humus, and the presence of these zeolites, the salts in these soils withstand weathering far better than they do in the podsols. All cultivated soils in damp climates belong to this brown earth type.

The conceptions "brown earth," "black earth" are some-what primitive; both these soils are types of "mull" soils; the brown earths are not stratified, while the black earths are somewhat stratified.

3. STEPPE SOILS

Let us now turn to a consideration of arid soils, and take as examples the steppe soils of Europe and Asia, studied by Wiegner (1921) and described by him as "semi-humid soils." This type of soil is to be found in Southern Russia, Siberia, Hungary, Bohemia, and many other regions on the outer side of the Carpathians, some of which border upon typically humid soil types. The prairies of North America fall into the same category. We shall confine our attention to the black earths (Tschernosens) of Russia, a type of soil rich in humus.

Fig. 57.—Typical profile of a "living" stratum of black earth. (*A*) Upper soil, (*B*) transition from upper soil to sub-soil, (*C*) sub-soil, (*D*) deposits of $CaCO_3$, (*E*) layer of low humus content, (*F*) and (*G*) layers rich in gypsum and humus, (*H*) layer of low humus content, (*J*) deep layer with deposited chalk, (*K*) top of the "dead" soil layer. (Wysotzki and Ramann.)

Since in these regions the evaporation exceeds the rainfall, the rain penetrates only to a limited distance in the soil. It is possible, then, to distinguish, with Wysotzki (Ramann, 1911, p. 540) an upper "living" layer, containing lower organisms and the roots of plants, from a lower "dead" layer, into which the rain does not enter, and up to which the capillaries of water from below do not ascend (Fig. 57).

The characteristic of the black earth is a high humus content, in coagulated form, together with a high clay content. Since a descending stream of water is not present, the products of mineral weathering remain in the soil. For this reason the humus materials are transformed by basic absorption into the neutral and coagulated state. There is no protective action of the colloid mineral materials, such as aluminium hydroxide and silicic acid. The silicic acids combine directly to form the exchange zeolites, of which clay is an example. These zeolites are regarded as colloidal compounds, in which the two components occur in varying proportions, though probably purely chemical combination

plays a part too. Van Bemmeln refers to such combinations as the "first step in a chemical reaction." It is sufficient for our purpose to know that the zeolites are colloidal gels, which are the agents in the so-called basic exchange.

In the presence of salts the negatively charged clay particles are flocculated—a process of great significance in the breaking up of the soil (Comber, 1922).[1] The flocculated zeolites are saturated with positive ions. The calcium zeolites are granular and allow the passage of water; the potassium zeolites are rather less so, while the sodium zeolites tend to a still greater degree of dispersion. The different physical conditions of precipitated zeolites are naturally of great import to the general state of the soil.

Different cations are held in the soil with different degrees of tenacity. The exchange zeolites, as a rule, retain potassium and ammonium with more force than they do sodium or calcium and magnesium. Potassium and ammonium are combined in the soil, and seem to be almost insoluble, while other ions flow through the soil more easily. It is for this reason that sodium is more plentiful in the sea than potassium.

Exchange processes in the soil take place somewhat as follows: when a soluble ammonium or potassium salt enters the soil, the sodium and calcium ions previously absorbed are replaced, and go into solution. The de-calcifying of a field by the addition of potassium fertilizer is commonly known in agriculture, and its effect can be traced to the stronger absorption of potassium ions as compared with ions of calcium.

Consideration must also be taken of the relative concentration of the ions; for with a great excess of calcium, the potassium can be thrown out of the soil.

The attraction for ions is not a property of the zeolites alone. The research of Van Bemmeln (1900) has demonstrated a complete homology between clay and humus as regards their ability to absorb ions. Humus itself is capable of retaining ammonium and potassium ions, beside others, such as the phosphate group. All the heavy metals are

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[1] Wiegner (Russell, 1927, p. 152) assumes that the clay particles in water are surrounded by a double electric layer. The outer layer is positively charged, and the inner layer (with complex $AlSiO_4$ anions) negatively charged. The changeable character of clay can then be explained by the splitting off of anions and cations from one or other of the layers.

absorbed to a high degree by the soil, and on that account are poisonous from the ecological standpoint.

Ramann (1911, p. 69) has summarized the conditions of absorption in a neutral soil as follows:

1. Phosphoric acid, potassium, and ammonium are strongly absorbed; chalk, magnesia, and sulphuric acid are only weakly absorbed; chlorine ions and nitric acid are not absorbed at all.

2. The salt added is completely taken up when part is combined and the other part separates out as an insoluble constituent, or when both the base and the metal form insoluble compounds.

3. Part of the salt is taken up when an equivalent amount of previously combined material goes into solution: this is the *base exchange* described above.

The occurrence of soil problems in agriculture has been discussed by Kleberger (1914–15), Ehrenberg (1918), Prescott (1916), Russell (1927, pp. 137, 151) and others.

Since the so-called "unsaturated" humus materials absorb from a neutral salt more of the basic component than of the acid, the solution becomes correspondingly acid. This is the cause of the acid reaction in acid humus soils, and to this cause has been attributed the acid reaction of peat (Baumann and Gully, 1909, 1911). The same conception has been applied by Harris to purely mineral soils (1914). A Michigan soil he investigated was found to colour litmus blue. An aqueous extract of the soil was neutral, but an extract with some salt like calcium nitrate gave an acid reaction. The subject has been fully discussed by Russell (1927, p. 182). Daikuhara (1914) has suggested that this is not simply a separation of the two ions of a salt, but that a base exchange takes place. The cation is exchanged with aluminium, which goes into solution to form a hydrolyzed acid salt.

The phenomena of absorption in the soil have been attacked from other standpoints (Rindell, 1911; Ehrenberg and Bahr, 1913; Odén, 1919; Ehrenberg, 1918). Baumann and Gully believed the acidity of acid humus to be due to the absorption of one ion of a neutral salt. These other investigators claim the existence of real humus acids, which dissociate partially to give hydrogen ions, and which can combine to form bases. Odén has asserted that these acids are soluble in water only with great difficulty. The fact that the acidity increases on the addition of a neutral salt, he explains by

saying that the salt displaces some of the hydrogen ions adsorbed upon the humus material.

The work of these investigators has not succeeded in explaining many of the peculiarities of the soil. It seems most probable that real acids should occur among the enormous variety of humus materials, a probability which is supported by Odén's investigations; and these acids could naturally form basic salts—humates. Moreover the humus materials, whatever their nature, are able to adsorb salts, by virtue of their colloidal properties, and this adsorption is often selective, for some ions more than others. The soil is such a complex mixture, that different investigators have probably experimented with totally different materials, a circumstance which may well explain the contradictions as to the selective adsorption of humus.

In the black earths, on account of the large quantity of salts, the humus is precipitated and present in a granular condition. A great part of the salts is adsorbed on the soil particles, and on account of this the osmotic pressure of the soil solutions is lower than it would otherwise be.

The rich mineral content of the black earths, combined with the increase of water content in spring, produces a rapidly developing rich vegetation, principally of grasses, though varying, of course, with the nature of the soil.

In the winter the soil is frozen, and in summer it dries out to such an extent that the decomposition of the humus is prevented. Some of the humus materials are taken into solution, washed down to a certain depth, and then precipitated in the clay beneath. In this way a horizon of humus is formed, which is the lower limit of the "living" soil. At the same level calcium carbonate is deposited, and often gypsum. The deposition of chalk usually occurs in two horizons, the lower of which may stand in some relation to the height of the water table. At higher temperatures, which increase the speed of weathering, and with low rainfall, the salts may even crystallize out from the soil; and in this way the "alkaline soils" of America are formed.

Under conditions favourable for decomposition, the humus is rapidly destroyed in arid soils. In an arid soil in America, Hilgard found a mean humus content of 0·91 per cent, while a damp soil had a content of 4·58 per cent (Hilgard, 1906). The humus of arid soils is far more valuable for plant life, since it is in a coagulated form, and offers an excellent sub-

stratum for bacteria.   For this reason an arid soil can be cultivated excellently when it has a humus content which would make cultivation impossible in a damper soil.

Arid soils whose salt content is not too high, are far more valuable for cultivation than are humid soils. They are richer in food materials; their physical constitution is more satisfactory; and, if sufficient water is present, they are better able to support a rich animal and bacterial population.   The limiting factors in such a soil are the relatively low water supply and the consequent high salt concentration.   Arid soils are typified by the perennial grass vegetation of the steppes, prairies, and savannahs.

Trees and bushes do not occur on real steppe or prairie. Under certain conditions, however, soils of the prairie type become colonized by trees.   The factors governing such a colonization are very obscure.   For a full discussion of this subject the reader is referred to Ramann (1911, p. 573), Clements (1929), and Warming-Gräbner (1915–18).

The above description of the two types of soils, steppe soils and the podsols, illustrates that the type of leaching which takes place in the soil is of the utmost importance.

The upper layer of a steppe soil is always liable to be leached out by the rain and the salts are precipitated beneath the surface.   The position of this precipitation region is characteristic of the arid soils.   It is very superficial; in extreme instances occurring even upon the surface.   As the soil becomes more moist, the depth of this storage layer sinks. Except in soils of high lime content pans injurious to the vegetation do not occur.

In podsols a similar accumulation of salts is to be found, but it is often in the form of pans, and is too deep to be reached by the roots of plants.

The reader's attention must be turned now to the study of soils in more detail: to their physical constitution, aeration, to the soil flora and fauna, and their interaction with the higher plants.

THE PHYSICAL STRUCTURE AND AERATION OF THE SOIL

1. MECHANICAL ANALYSIS OF SOILS

Upon the physical nature of the soil depend a number of fundamental properties: the power of absorption, the water-holding capacity, and the aeration. The determination of the physical structure, therefore, is of importance if one is to assess the value of the soil in ecology or in agriculture.

The problem is by no means simple, for the soil consists of a mixture of different substances. This mixture has been divided into two great groups: the humus, and the mineral constituents.

The humus materials are gels of very variable dispersion. It is impossible, in the present state of our technique, to estimate directly the physical condition of humus colloids. The humus content alone (usually estimated by combustion; Robinson, 1927) means very little, for it has already been pointed out how different is the effect of the same amount of humus in a podsol and a steppe soil. The reaction of the humus is of some importance, since it throws some light upon the degree of dispersion of the colloids. The concentration of salts and of certain ions is also of importance in an investigation of the colloidal condition.

Humus always occurs in macroscopic "flocks" or aggregates. It is clear that the size and distribution of these aggregates, even when the total amount present is constant, will influence differently the degree of aeration and water-holding capacity of the soil. A very finely divided humus imparts to the soil an impervious structure, and a coarser humus promotes drainage.

Finally, it should be borne in mind that it is in the humus layer of the soil that the fungal and bacterial population is to be found, so that both the chemical nature of the humus and its mechanical condition will exert an influence upon the soil

flora.   It is obvious that the mere determination of the amount of humus in the soil gives no idea of its ecological significance. New methods for the analysis of humus are necessary, and these methods have not yet been discovered.

With regard to the mineral constituents of the soil, the problem is somewhat similar.   Some of the mineral particles occur as gels, as, for instance, the very fine particles which compose clay.   These fine particles form a suspension with the soil water, and the degree of dispersion varies, according to the ions present and the salt content, from particles of ultra-microscopic size to particles visible under the microscope. The reversible process of flocculation of clay can easily be studied in a test-tube.   Now the concentration of ions in the soil, upon which the state of dispersion of the clay depends, varies continuously throughout the year according to the concentration of the soil water and the temperature.   Without a knowledge of the yearly fluctuation of these factors, one has no certain information as to the physical condition of the clay in the soil.   A mechanical analysis of the soil, therefore, has a very limited application.   The main significance of such an analysis is that it gives some idea of the physical "capabilities" of a soil.

A detailed description of the special methods used in the mechanical analysis of a soil cannot be given here.   In outline, the method for the analysis of clay is as follows: A soil sample, previously sifted and freed from humus by heating with nitric acid (Atterberg, 1912, 1913), is made into a suspension with distilled water.   The suspension is allowed to stand, and the soil particles sink to the bottom, the larger falling more rapidly than the finer particles.

The time required for a particle to fall bears a definite relation to its diameter.   Clay particles are irregular in shape, but calculations assuming them to be spherical show that the time required for a particle of from 0·2–0·02 mm. diameter to fall 20 cm. is 32 seconds, while particles from 0·02–0·002 mm. in diameter require about 9 minutes (Novák, 1916). The finest fractions, which comprise true colloidal clay, require days or weeks for their sedimentation.

Odén (1916) evolved an automatic method of measuring the size of soil particles.   Very careful analysis of a clay gave a continuous curve (Fig. 58).   The limiting factor in the experiments is the very long time taken for the finest particles to settle.   If the apparatus were modified to be used with a

centrifuge, this limiting factor might be to some extent eliminated.   The ideal distribution curve, which Odén's method nearly attains, is naturally continuous.   For practical purposes, a definite scale of dimensions is used.   Several such
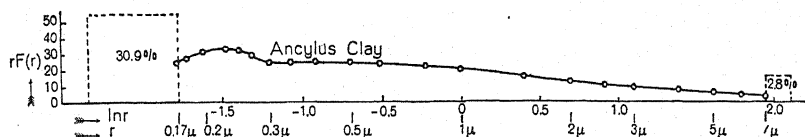
FIG. 58.—Distribution of non-colloidal particles in an Ancylus clay, determined by Odén's method.

scales have been put forward.   The English and American systems have been discussed by Russell (1927, p. 122, Table XXXII).   Atterberg's system is perhaps the simplest; he distributes the fractions as follows:

Gravel .	over 2 mm. diameter.
Sand .	. 2·0 —0·2 mm.
Fine sand .	. 0·2 —0·06 mm.
"Flour" sand.	. 0·06 —0·02 mm.
Coarse silt .	. 0·02 —0·006 mm.
Fine silt (dust) .	. 0·006—0·002 mm.
Clay .	less than 0·002 mm.

This basis is not altogether arbitrary, nor yet are the figures chosen merely on account of their symmetry.

The diameter 0·002 mm., taken as the upper limit of the clay fraction (the same limit is taken in the English nomenclature), marks an important limit in the colloidal properties of the material.   For when clays reach a degree of dispersion of 0·002 mm. they behave as suspension colloids.   They are very sensitive toward small quantities of electrolytes and hydrogen ions; these cause flocculation, which process is reversed on the removal of the ions.   Hydroxyl ions, on the other hand, stabilize the dispersed state of the clay.   The clay, in fact, behaves like a negatively charged colloid.

A remarkable property of clay is its plasticity when damp. The particles cohere together, and when present in the soil in small quantities, they increase its water-holding capacity, though when clay is present in excess, the soil becomes very heavy.   It is well known that a layer of clay is almost impervious to water.   When the clay is dry it becomes very hard, and shrinks, with the formation of cracks in the soil.   A high percentage of particles as small as 0·002 mm. diameter in the soil is disadvantageous for agriculture; in fact, heavy clay

soils can be quite unproductive. According to Russell, the clay content of a good agricultural soil should be no more than 8–16 per cent. According to Ramann, the proportion should be as high as 20–30 per cent.

A moderate clay content is one of the most important requirements in the formation of a fertile soil. It has already been pointed out that the clay and humus in the soil are the centres of the absorption and exchange processes.

Particles of silt in the soil, of diameter 0·002 to 0·02 mm., also retain certain colloidal properties, and are precipitated by electrolytes.

According to Comber (1920), there is some difference between clay and silt. The behaviour of the silt particles is that of an ordinary suspension of particles insoluble in water, while the clay particles are said to be coated with a layer of emulsoid silica, which confers upon the system properties similar to that of an emulsoid colloid. On this assumption can be explained the different behaviour of clay and silt toward electrolytes. The precipitation of a silt suspension occurs most rapidly at the isoelectric point, while that of a clay emulsion is most rapid in slightly alkaline solution, for the (OH) ions are said to break down the protective emulsoid. Such a difference in the properties of silt and clay might be of significance in nature.

Particles of diameter greater than 0·02 mm., as Hilgard has pointed out, do not exhibit any of the peculiarities of clays. Particles of this size begin to be visible to the naked eye, and the root hairs are able to penetrate between them. Clay, on the other hand, is so thick in consistency that root hairs are unable to penetrate into it.

Coarse silt, of diameter 0·006 to 0·02 mm., prevents the clay particles from becoming too closely compacted together, and is for this reason a most valuable constituent of clay soils. In fact, the fertility of a soil is to a great extent dependent upon the presence of suitable proportions of clay and silt. Many of the best loams contain from 30 to 40 per cent of coarse silt, which is largely responsible for the drainage and aeration of the soil.

The fine and coarse sand in the soil, which Kraus (1911) calls the "soil skeleton," also promotes the drainage and aeration of the soil. If sand is present in the soil in too great a proportion, however, the water capacity and the ascent of soil water by capillarity are reduced. Excess of sand also

bespeaks poverty of mineral nutrition, especially when there is very little humus present, or when it is present in a highly dispersed form.   As the clay content of a soil diminishes, the humus in the soil becomes more and more important for its fertility, on account of the resemblance between the physico-chemical properties of humus and those of clay.

The significance of colloids in the soil depends upon their enormous internal surface, which is the seat of chemical changes, and upon which essential ions are held in the soil. Even the bacterial numbers in the soil are related to the internal surface.   Analysis of the clay gives some idea of the extent of the internal surface.   An indirect method evolved by Mitscherlich has been described on page 114.   It will be remembered that this method did not yield very consistent results.   The colloidal content may also be determined from the adsorption of dyes or of gaseous ammonia (Gile, 1924; 1925), or from the actual heat of adsorption (Anderson *et al.*, 1922; 1924; 1926).

If the soil particles were all of the same size, and spherical in shape, they would fall into a symmetrical arrangement when compacted into a layer.   It would be possible to calculate the size and form of the interstices, and consequently the degree of aeration of the soil, from the size of the particles alone.   Soil particles, however, are of many different sizes and shapes; and even if their mechanical composition is the same, two soils may exhibit totally different conditions of aeration, owing to the different states of aggregation of the particles.   It is necessary to consider, therefore, not only the structure of the individual particle, but also that of the aggregate.   The act of ploughing a field affects both its aeration and its drainage.   The question of drainage has already received some attention; it remains now to discuss aeration.

2. THE AERATION OF THE SOIL

Bacteria, fungi, insects, and the roots of plants in the soil use up oxygen in respiration, and produce a corresponding amount of carbon dioxide.   Since the provision of oxygen and the removal of carbon dioxide depend entirely upon diffusion to and from the atmosphere, the concentration of these two gases in the soil will depend upon the intensity of respiration and the resistance to diffusion in the soil.   If the soil is highly impervious to diffusion, the aeration is bad; the oxygen concentration decreases, and an accumulation of carbon dioxide

follows. The intensity of respiration depends upon the partial pressure of oxygen, and upon the respiration depends the growth and vigour of the whole plant. An excess of carbon dioxide, moreover, is poisonous to the plant. It is clear, then, that aeration is a factor of the first importance in ecology.

Not all plants react in the same way to a shortage of oxygen. A decrease of a few per cent in the concentration of oxygen will cause a decrease in the growth of Coleus (Cannon and Free, 1917; Cannon, 1924) and in cereals (Janert, 1923). Some species of willow, on the other hand, will live for weeks without oxygen in the soil. Clements (1921) and Romell (1922) have published observations upon the sensitivity of various plants to carbon dioxide. Swamp plants and moorland plants send their roots into a medium almost free from oxygen, and yet they seem quite resistant to the oxygen shortage.

There is the same specificity in the reaction of plants to higher concentrations of carbon dioxide. The growth of most mesophilous plants begins to fall off when the concentration of carbon dioxide reaches 1 per cent (Lundegårdh, 1923, a; 1924, a; p. 163, for literature). Some fungi and bacteria, on the other hand, can endure very high concentrations without any ill effect (Brown, 1922; Lundegårdh, 1923; Plummer, 1917).

Upon the seeds of many plants, as Kidd has shown (1914; 1915; 1917), carbon dioxide acts as a narcotic. Germination is inhibited, though the power to germinate is regained when the carbon dioxide is removed. On the whole the carbon dioxide content of a soil and the oxygen content will vary inversely, so that it is often very difficult to decide which of these two factors is inhibiting plant growth. There exist scarcely any quantitative experiments in which the ecological effect of aeration has been studied. The effect of aeration upon the welfare of plants in water cultures has received considerable attention from Knight (1923), Hall and others (1913), and Livingston and Free (1917). In estimating the aeration of a soil from the ecological standpoint three determinations have to be made: the concentration of oxygen and carbon dioxide in the soil atmosphere, and the rate of diffusion of gases in the soil. Since the concentrations of oxygen and carbon dioxide vary inversely, it is sufficient to work with one of these factors. Carbon dioxide is chosen because its influence upon plant growth is apparent at very small concentrations: plants are more sensitive to the

presence of carbon dioxide than they are to the absence of oxygen.

As the following figures show, the concentration of carbon dioxide increases with increasing depth below the soil surface:

Grass soil . . 1·46% CO_2 at 15 cm.; 1·64% at 45 cm. (Russell)
Arable soil . . 0·34% „ 15 cm.; 0·45% „ 45 cm. „
Beechwood soil . 0·33% „ 30 cm.; 0·39% „ 60 cm. (Romell)
Sand . . . 0·25% „ 15 cm.; 0·31% „ 30 cm. (Lundegårdh)

Observations upon the concentration of carbon dioxide in the soil atmosphere have been made by Lau (1906); Vageler (1906), who worked upon moorland soils; Russell and Appleyard (1915; 1917); Romell (1922) and Lundegårdh (1924, a, p. 167). Fodor (1882) found that at still greater depths, from 1 to 4 metres, the concentration varied from 1 to 4 per cent, and even reached values as high as 8 per cent. As would be expected, the aeration decreases with the depth of the soil; though it does not decrease indefinitely, for the production of carbon dioxide is most abundant in the surface layers, where the majority of soil organisms are to be found. The greatest activity occurs in the upper 10–30 cms. and many soils at a depth of one metre are almost sterile. (For the relevant literature, see Lundegårdh, 1924, a, p. 151). Some idea of the falling off in activity as the depth increases is given by the following analysis of a sandy soil: The amount of carbon dioxide produced per hour, from a column one square centimetre at the base, and—

0–10 cm. high = 0·0502 cc.
10–20 cm. „ = 0·0155
20–30 cm. „ = 0·00296
30–40 cm. „ = 0·00166

The table above illustrates the fact that the carbon dioxide concentration at a given depth varies markedly in different soils; for it depends partly upon the soil respiration and partly upon the resistance to diffusion. The latter, as the author has shown, fluctuates far more than the former. In cultivated unmanured soils the absolute production of CO_2 lies within narrow limits, 0·2–0·4 grams per square metre per hour, while the concentration of carbon dioxide in the soil, at a depth of 15 cm., can vary within wide limits, even at different times in the same place. This fluctuation is related to the changing water content in the soil. The more water there is in the soil, the less free air space is there, and the greater is the resis-

tance to diffusion. An air-dry soil contains 50 to 60 per cent of air by volume. With a water content of 25 per cent, the air space is halved, so that the resistance to diffusion is doubled. If the amount of carbon dioxide which diffuses through 1 cubic centimetre in one second be denoted by K, and if this be taken as a measure of the aeration of a soil of thickness y_2, then, approximately:

$$K = \frac{(a_2 + a_3) \times y_2 \times 100}{3600 \times (b_2 - b_1)}$$

where $(a_2 + a_3)$ is the amount of carbon dioxide diffusing through the layer y_2 in cc. per area of 1 sq. cm. per hour, and b_2 and b_1 are the concentrations of carbon dioxide above and below the layer. Methods for determining aeration have been described by Lundegårdh (1922, b, 1924, a, p. 156). Hutchins and Livingston (1923,) have evolved an indirect method which involves the colorimetric estimation of the diffusion of oxygen through a porous vessel (*see also* Hutchins, 1926).

The carbon dioxide which diffuses from the soil is determined as follows: with a specially constructed borer samples of a definite cubic content are taken from the soil, first from the upper ten centimetres, then from the ten centimetres below that, and so on. These samples are taken to the laboratory in airtight containers. Here they are put into flasks kept at 18° C. and the amount of carbon dioxide liberated from each of the samples after twenty-four hours is measured.

In the field the amount of carbon dioxide in the soil atmosphere can be measured by inserting a metal tube ten, twenty, and thirty centimetres into the soil, and sucking out a certain volume of air into a portable gas analysis apparatus. The papers of Russell, Romell and Lundegårdh, cited above, give further details as to these methods. The carbon dioxide content alone cannot be regarded as a measure of the aeration of the soil (Lundegårdh, 1924, a).

The limit of normal aeration is considered to be reached when the carbon dioxide at a depth of 15 cm. reaches a percentage of 1. If the rate of carbon dioxide production is 0·4 gm. per cubic metre per hour, the value of K is 0·009. Among a number of sandy loams in Sweden, with varying contents of humus, the values of K lay between 0·010 and 0·060. For the most part these soils are well aerated.

Very often, owing to intensive manuring or high rainfall, the production of carbon dioxide increases, and the coefficient

of diffusion falls below that of normal aeration.   When the concentration of carbon dioxide exceeds 1 per cent toxic phenomena appear: the germination and growth of wheat seedlings are retarded.   This, however, is the lower limit, and other plants are not affected by such concentrations.   A concentration of 1–2 per cent of carbon dioxide, extending over a week or a fortnight, will produce pathological symptoms in lettuce, turnip, and oats.

Where the value of the diffusion coefficient K of a soil is below 0·009, steps have to be taken to increase the aeration of the soil; by tillage, by liming, or by other means which increase the friability.   Where the water content is too high, the soil must be drained.   It is very probable that the diffusion coefficient is of the greatest importance in the formation of natural plant communities, though this aspect of ecology has received scarcely any detailed attention.   As the value of K diminishes, those plants are eliminated which are most sensitive to carbon dioxide poisoning and to deficiency in oxygen. Finally there remain only those plants which can live in a soil with scarcely any aeration.   For germination, too, the aeration of the soil is of great importance; it is clear that seeds buried too deeply in the soil would be in an atmosphere of carbon dioxide which is toxic.   Kidd (1915) has pointed out how many seeds lie dormant in the earth for years, and only germinate when, by some chance or other, they come to the surface of the soil.   The flora which appears in a freshly cleared wood undoubtedly comes to some extent from old seeds, which germinate partly on account of the better illumination, and partly on account of the increased aeration due to drying out of the soil.

In a cultivated field, the concentration of carbon dioxide in the soil atmosphere is markedly increased by manuring. Too intensive manuring of a good field can depress the aeration of the soil below the normal, and bring great harm to the crops growing in it.

The oxygen content of the water table is also of great importance, and it depends to some extent upon the aeration of the soil above.   According to Hesselmann, damp moorland soils are almost free of oxygen; and the water which percolates through the soil of a wood loses a great proportion of its oxygen.   Stagnant water most frequently suffers from lack of oxygen, and the foul products formed in it are due to this oxygen shortage.

The dependence of aeration upon the physical structure of the soil is illustrated by an example from Howard. When an impervious soil at Pusa, India, was mixed with pot-shard or sand, an increase of from 10 to 20 per cent in the yield of wheat, oats, and tobacco was obtained. Hall, Brenchley, and Underwood obtained similar results in pot-culture experiments with soils of different physical consistencies (Russell, 1927, p. 65). The work of Howard showed conclusively that the increased yield was due to an enhanced aeration of the soil. When aeration was increased by reducing the irrigation instead of loosening the soil, the same result was obtained.

The following figures give some idea of the sharp local differences in aeration and the carbon dioxide content of the soil which occur in nature. They were taken at the edge of the Alder swamp reproduced in Plate IV.

Association.	CO_2 Content at a depth of 15 cm.
Oxalis acetosella, Maianthemum bifolium, Melandrium rubrum	0·24–0·50%
Carex vesicaria, Peucedanum palustre	1·24%

The two habitats were only two metres apart. It seems very probable that the plants of the first association were unable to advance further toward the edge of the swamp, on account of the bad aeration of the soil. Other instances of zonation around lakes and moors undoubtedly depend upon the aeration, yet this factor is often overlooked, and has never been carefully measured. It must not be assumed, on the other hand, that this factor is the dominant one. The growth of a plant in such a habitat will depend upon the resultant effects of water and aeration upon the plant.

The interrelation between aeration, soil constitution, and rainfall, can be generally expressed as follows: the more impervious the soil, the sooner is the limit of normal aeration reached with increasing humidity of the climate.

In a dry climate, plants very sensitive to aeration will grow in a soil which is highly impervious: the soils of steppes might be cited as an example. In Northern Europe, on the other hand, where the climate is damp, the heavy peat soils tend to become boggy, and support only a flora of plants resistant to poor aeration. In very damp climates, therefore, ordinary plants prefer soils with a loose structure, such as the sand soils and mould soils of the temperate climate. In spite

of their high water capacity, mould soils are very loose in structure, so that although the production of carbon dioxide is high it does not accumulate in the soil. This is only another illustration of the importance of the state of aggregation of a soil; in these mould soils the aeration and the drainage are good, yet the water-storage capacity is not impaired. It is for these reasons that a good mould soil represents the optimum of edaphic conditions.

Probably even the best mould soil of the temperate regions would become badly aerated in the tropics, owing to the greater humidity and heavy rainfall. The soil of a tropical rain forest contains very little humus; it consists principally of mineral particles, so that its aeration is probably good, and this, no doubt, is a contributing factor to the luxuriant vegetation. Plants growing in clay soils in the tropics are only able to develop to their full when they are provided with special organs for root respiration. It seems most probable that aeration as a limiting factor is found more frequently in warmer than in cooler climates.

CHAPTER VII

CHEMICAL PROPERTIES OF THE SOIL

1. The Physiological Effects of Nutritive Salts

ACCORDING to the older ideas in plant physiology, the so-called "indispensable" nutrient salts were those whose function was to build up the plant body. As applied to nitrogen, derived from nitrates or ammonium; to sulphur, derived from sulphates; and to phosphates, this conception is quite clear. These elements are the essential constituents of the proteins and phosphatides which form protoplasm, and are therefore as important to the plant as the carbon derived from the air. In addition to these, other elements, calcium, potassium, magnesium and iron, are essential to the plant's welfare; but very little is known as to what part these play in the chemistry of the plant. In recent years there has been attributed to the salts the function of maintaining the colloidal state of the protoplasm and the cell membrane, so that their function might be regarded as physical rather than chemical. The literature upon this subject has been summarized by Benecke-Jost (1924, I, p. 139).

The study of the antagonistic action of ions began with the observations of Loeb (1906) upon marine organisms. Subsequently a great deal of work was carried out upon plants, all of which work emphasized the enormous importance of certain *combinations* of ions for the life of plants. (*See* Osterhout, 1906; 1907; 1908; 1914; Hansteen-Cranner, 1910; Szücs, 1913; Stiles, 1926.) We now know that apparently harmless salts, such as potassium and sodium chlorides, when present in the pure state, even in very dilute solutions, will rapidly bring about poisoning and death. (*See* authors quoted above, and Lundegårdh, 1911; Cholodny, 1923.) A minute quantity of calcium chloride added to the solution removes the toxic action, and in such a solution a plant will grow normally. The calcium ion is particularly important as a "buffer agent," for it destroys the toxic effect not only of

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sodium and potassium, but also of magnesium, which is other-
wise very poisonous.   It is this antagonism of calcium and
magnesium which is most commonly recognized in agriculture
(Kleberger, 1915; Gericke, 1922).   It occurs not only for the
higher plants, but also for fungi (Lundegårdh, 1924, c,) and
bacteria (Lipman, 1914; Greaves, 1920).   With the exception
of the *Cyanophyceae*, however, most of the lower plants seem
to be able to live without calcium (Pringsheim, 1926).

It is an interesting fact that when the concentration of one
ion is kept constant, and the concentration of the other is
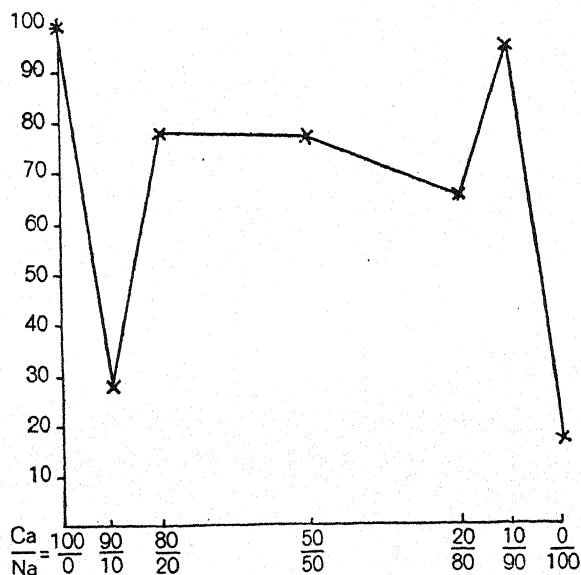
FIG. 59.—The influence of different combinations of calcium and sodium upon the growth
of Dala oats.   (After Philipson, 1925.)

varied, the effect of successive combinations upon growth fol-
lows a periodic curve (Fig. 59).   (*See* Hansteen-Cranner,
1908; Waynick, 1918; Reed, 1918; 1923; Philipson, 1924.)
That is to say, there are several combinations of calcium and
magnesium which have the same effect upon the growth of
the experimental plants.   The effect of one ion upon the
permeability of the cell to another depends upon the relative
concentrations of the two ions (Lundegårdh and Morávek,
1924; Iljin, 1928).

This antagonistic action of ions is interpreted as an adsorp-
tion phenomenon.   Potassium ions, for instance, in a pure
aqueous solution, are so strongly adsorbed that they injure

the colloidal condition of the cell.   Since, however, the calcium
ions are also adsorbed, there is a mutual displacement, when
both ions are present, from the surface of the cell wall.
When the two ions are present, according to the theory of
Michaelis and Rona, neither can monopolize the cell sur-
face, and the effective concentration of either ion is therefore
diminished.   In a good nutrient solution, the various ions are
present in such a proportion that they mutually restrict one
another's adsorption.   In fact the chief function of some
nutrient materials may be that they prevent the excessive ad-
sorption of others (Hoagland, 1923).   Morita and Livingston
(1920) found that young wheat plants would flourish without
calcium, so long as the phosphate concentration was low.

   According to modern ideas, protoplasm is a mixture of
emulsoids and suspensoids.   It is clear that the degree of
dispersion and the state of imbibition of the protoplasm will
influence the nature and the rate of the chemical changes
which take place within it.   But the condition of the colloids
is in turn influenced by the adsorption of ions; so that indirectly
the ions absorbed can exert an influence upon the chemical
processes in the protoplasm.

   The effect upon growth of many salts which do not
belong to the group of essential elements can be explained
from the standpoint of colloidal chemistry.   Aluminium,
which promotes growth, when present in small quantities
(Stoklasa, 1922), probably has the same function as calcium,
since it will remove the toxic effect of other ions by reason of
its strong colloidal properties.   Such an antagonism has
already been demonstrated toward copper (Szücs, 1913) and
iron (Stoklasa, 1922).   In higher concentrations aluminium
itself becomes toxic: the curve of antagonism (Fig. 60) has
an optimum at a concentration of 0·15 normal aluminium.

   Even the heavy metals, copper, zinc, and mercury, which
are highly toxic, even in dilute solutions, will stimulate growth
if they are present in sufficiently small quantities.   This
phenomenon has been described with many fungi and higher
plants.   The literature upon the subject will be found in
Czapek's book (1922), in Benecke-Jost, 1924.   (*See also*
Lundegårdh, 1924, *e*; Stewart and Smith, 1922.)   Zinc is
apparently essential for the growth of *Aspergillus niger* (Roberg,
1928), and boron seems to be necessary for the normal
development of *Leguminosae* (Warrington, 1923; Brenchley
and Thornton, 1925).   The action of these ions is always

specific—a property which Boas (1928) has applied to the separation of fungi and bacteria.

The curve of growth obtained when increasing quantities of heavy metals are added to the nutrient solution is apparently not a simple optimum curve, but is periodic in shape (Lunde-
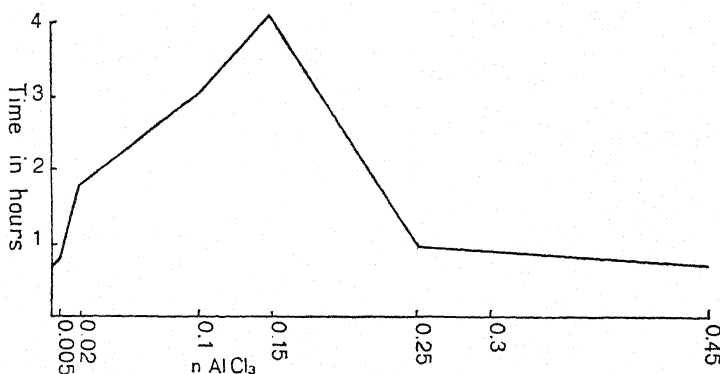
FIG. 60.—The inhibition of the poisoning effect of 0·025 N. copper sulphate by aluminium chloride.   The toxicity was measured from the suspension of the geotropic reaction of cucumber hypocotyls.   The ordinates denote the time after which 70 per cent of the hypocotyls do not react.   (After Szücs, 1913.)

gårdh, 1924, e).   In very small quantities the metal exerts a limiting action; as the concentration increases it actually promotes growth, and with further increase in concentration the inhibitory effect reappears (Table XXXI and Fig. 61).
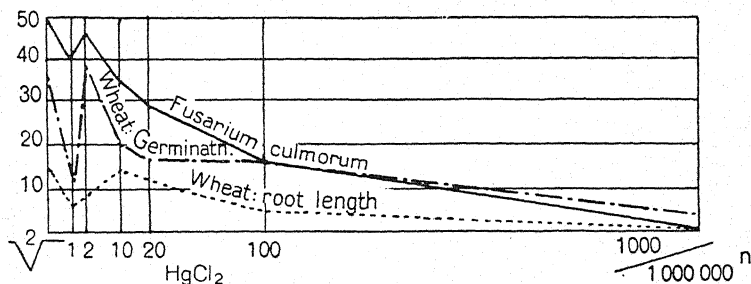
FIG. 61.—The germination and the root growth of wheat, and the growth of *Fusarium*, in mercuric chloride at different dilutions.   (Lundegårdh, 1924.)

The author also determined the absorption of Cu-ions by grains of wheat.   After exposure to the copper, the seeds were laid out to germinate.   It was observed that the time curve of absorption was periodic, and this periodicity was reflected in the growth of the seedlings.

TABLE XXXI

GERMINATION AND ROOT GROWTH OF WHEAT IN SOLUTIONS OF $HgCl_2$

Concentration of $HgCl_2$	$\dfrac{N}{\infty}$	$\dfrac{N}{1,000,000}$	$\dfrac{N}{500,000}$	$\dfrac{N}{100,000}$	$\dfrac{N}{50,000}$	$\dfrac{N}{10,000}$	$\dfrac{N}{1,000}$
Germination .	36	15	40	19	16	17	4 per cent
Length of root	10–20	2–8	4–8	5–18	5–12	2–5	0–2 mm.

This periodic absorption of ions is suggestive of the Liesegang phenomena of colloidal chemistry, and the present writer is of opinion that the ions enter the colloidal covering of the seed with a periodic "ebb and flow," or layer by layer; which would explain the periodicity of absorption. The occurrence of Liesegang phenomena in seeds was actually observed by Möller (1921) in the entry of silver nitrate into wheat seeds. The same interpretation might also be applied to the adsorption of ions on the cell wall and the cell membrane, for it would explain some of the periodic phenomena observed in antagonism. In 1915 Pantanelli showed that the uptake of ions by the plant cell probably followed a periodic time curve. The work of Tisdal in the writer's laboratory, where wheat was grown in water cultures, demonstrated that the uptake of potassium with increasing concentration of potassium in the medium, followed a double optimum curve (Fig. 62).

To revert to the effect of the heavy metals on growth, it is worthy of note that the rate of metabolism, and the rate of respiration both increase under the influence of the ions of the heavy metals (Pringsheim, 1914; Lundegårdh, 1924, e). The metallic ions are adsorbed on the protoplasm, and increase thereby its adsorptive power for certain other substances. Warburg's experiments have indicated that respiration is an adsorption reaction, taking place on a protoplasmic surface where iron is present (Warburg, 1921; 1922). Treatment with copper also increases the rate of respiration, so that it is possible that copper may effect a similar activation of the surface.

The toxic action of the heavy metals in greater concentrations is probably due to their denaturation of the plasma colloids. The action of aluminium upon the protoplasm is exactly the same as its action upon a non-living gel. In low concentrations it precipitates the colloid, in somewhat higher

concentrations of aluminium no precipitation takes place, and in higher concentrations still, the colloid is precipitated (Szücs, 1913). This wave form of precipitation curve is a general phenomenon in colloid chemistry, and this may well be the explanation of a great many periodic phenomena in physiology.

The uptake of ordinary nutritive salts depends to a great degree upon adsorption. A paper by the present writer published in 1911 pointed out how the permeabilities of the different salts bore some relation to the additive series known
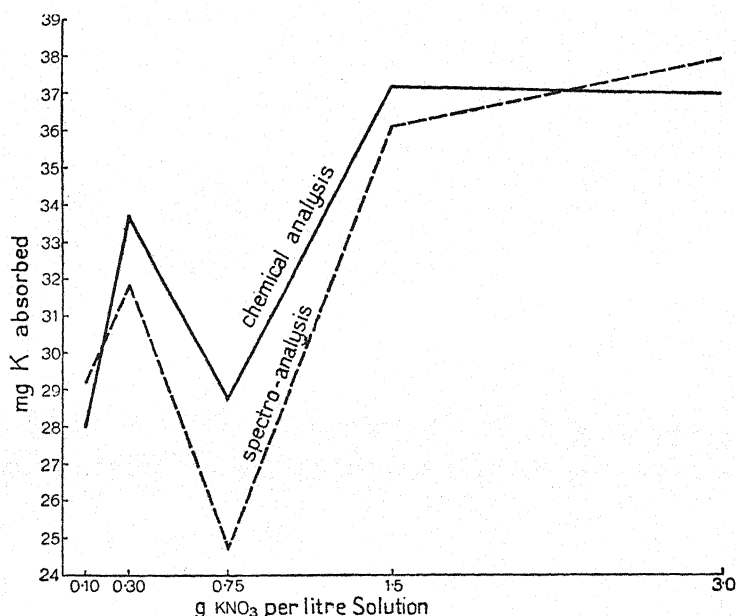
FIG. 62.—The uptake of potassium by wheat seedlings, from solutions of differing potassium concentration. The results of both chemical and spectro-analyses are given. (After Tisdal, see Lundegårdh, 1929.)

in colloidal chemistry. Subsequently Kahho (1921), using the same method, found that the uptake of salts from tenth normal solutions over short periods depended wholly upon adsorption.

Pantanelli carried out experiments extending over eight hours, and measured the amounts of salts taken up by chemical analysis. He confirmed the earlier discoveries of Nathanson and Meurer, namely, that ions rather than whole salt molecules are absorbed. It is very rarely that an equal number of anions and cations are taken up from the same salt. Hoagland

(1924) and others have confirmed this view. As Hoagland has pointed out, the absorption of ions is frequently a question of exchange; the plant takes up an [NO₃] ion, and a [CO₃] ion is withdrawn from the roots in its place. This does not always occur, however, and frequently as a result of selective absorption, the concentration of [OH] or [H] ions in the solution is altered. Unbalanced manuring of a soil with sodium nitrate leads to alkalinity of the soil because the plant absorbs more nitrate ion than sodium ion. Conversely, over-manuring with ammonium sulphate produces an acid reaction, on account of the predominant absorption of ammonium ion. The energy necessary for separating two constituent ions of a salt is provided by the absorption potential.

Since the intensity of absorption depends upon the state of imbibition of the protoplasm, negative absorption can occur, i.e. the secretion of previously absorbed ions. Pantanelli has brought forward evidence of such a secretion, and it is supported by experiments carried out by Morávek and the present writer (Lundegårdh and Morávek, 1924). Possibly it is this interaction between the two processes, the absorption of ions and imbibition, which is responsible for the extraordinary periodic phenomena in the uptake of ions, observed by Pantanelli. The present writer has recently found a distinctly periodic absorption of copper ions by wheat seeds. This is obviously only a special instance of the Liesegang phenomena, caused by the diffusion of a salt solution into a hydrogel.

Colloidal phenomena are of still further importance in the uptake of salts, for the permeability of the cell membrane is influenced by ions. Not only is an ion taken up according to the measure of its adsorption, but when taken up, it influences the rate of uptake of other ions (Fig. 63). Certain ions, such as [NO₃], are rapidly absorbed, and facilitate the absorption of other ions, while the absorption of aluminium inhibits the absorption of other ions. The behaviour of various ions differs according to the combinations in which they are present, which implies that other processes play a part in absorption.

The uptake of ions, therefore, and their effect upon the permeability of the cell, is bound up with their adsorption upon the protoplasmic membrane. It seems to be generally true that the more colloidally active a substance is, the less of it is absorbed (Kahho, 1921). The monovalent ions of the

alkali metals and the nitrate ions penetrate most readily; the precipitating power of these ions is weak and, as a rule, they facilitate the uptake of other ions. The bivalent ions magnesium and calcium penetrate very slowly, and frequently these ions decrease the permeability for other ions following them. If the uptake of sodium from sodium nitrate and sodium sulphate be measured, it will be found that more sodium is absorbed from the former salt, for the $[SO_4]$ group in the latter hinders the uptake of sodium.

The matter might be represented as follows: ions which are active toward colloids lower the degree of dispersion; the particles become to some extent aggregated, or the state of imbibition is changed, so that the adsorptive surface is reduced. Hansteen was even able to observe with the ultra-microscope the precipitating action of calcium upon protoplasm (Hansteen-Cranner, 1922). Monovalent anions and cations either exert no influence upon the degree of dispersion of the plasma colloids, or actually increase the dispersion: thereby increasing the internal surface and the adsorptive power.

FIG. 63.—The influence of NO'_3 (as the sodium salt), Ca'' and Al''' (as chloride) on the uptake of potassium. Experiments extending over three days with wheat seedlings. The rate of uptake of potassium in the absence of other ions (except Cl') is denoted by 100. (After Lundegårdh and Morávek, 1924.)

Most of the methods for measuring permeability are satisfactory over short periods, but would be quite unsatisfactory for determinations under natural conditions, where the absorption continues over long periods of time, and where there is the active interference of other ions.

In a number of pot-cultures of cereals set up in the writer's

laboratory, in which the plants grew in quartz sand watered with the culture solutions, an inverse ratio between nutrients given and the ash content of the seed was often found. There seems to be a definite antagonism between calcium and magnesium, and between calcium and potassium, so that with the addition of calcium less magnesium and potassium are taken up. The same antagonism has been observed by Ginsburg (1925). The secret of a "suitably balanced" nutrient solution, then, depends probably upon there being the right relationship between the various ions present.

The results of flooding a tissue with excess of one nutrient salt has been followed, up to the present, only for chlorides. It may be conjectured that certain so-called "physiological diseases" are due to inadequately balanced nutrient solutions.

Since the various individual salts influence one another in their action upon protoplasm, in the manner described above, it would not be expected that the same growth curve would always be obtained by varying a particular nutrient salt. On the contrary, the shape of such a growth curve would depend upon the quality and concentration of other ions present in the substratum.

As far as concerns the purely chemical effect of salts, and their function as constituent elements of the plant body, one would anticipate relationships similar to those already known in carbon dioxide assimilation. The variation of a single factor, while others remained constant, gave a curve which, though it could not be treated mathematically, conformed to a general "logarithmic" type. The relationship which the curve conveys may be expressed for the purposes of ecology as follows:

The more nearly a factor is in minimum in relation to the other factors acting upon the plant, the greater is the relative influence of a change of that factor upon the growth of the plant. As a factor increases in intensity, its relative effect upon the plant decreases; and when the factor is in the region of its maximum the effect of a change upon the plant is nil.

This "law of relative effects" (Relativitätsgesetz) for the factors acting on assimilation is in complete agreement with the findings of Mitscherlich concerning the action of the chemical factors upon plant yield (Mitscherlich, 1920). To this relationship Mitscherlich gave the name "Wirkungsgesetz der Vegetationsfactoren." It is clearly another instance of the law of relative effects, and to Mitscherlich must be

given the credit for having enunciated this law for the chemical factors with such exactitude.   Similar relationships have been found by Wolff (1877), Hellriegel *et al.* (1898), for higher plants, and by Pringsheim (1914) for fungi.

The lively interest aroused by the work of Mitscherlich can readily be understood; for he has presented the work in a most attractive mathematical form, and it is obviously of the greatest importance in the study of the use of fertilizers. His results are expressed in the following formula (Mitscherlich, 1920; also Boresch, 1928):

$$y = A (1 - e^{-cx})$$

where $y =$ the yield, A is the maximal yield, x is the intensity of a factor in the environment, and c is constant (the "Wirkungsfactor").

The formula is discussed by Mitscherlich (1920, p. 5), Baule (1920), Rippel (1922), Romell (1924), and Briggs (1925).

Judging from the work of Mitscherlich and others, this formula has a very extensive application; though it has been objected (Briggs, 1925; Söding, 1928; Lemmerman *et al.*, 1928) that the formula is not of general application; this, however, is a point which cannot be decided without further experiment.   It is not desirable to place too much confidence in the mathematical equation, for the smooth curves obtained in laboratory experiments occur only rarely in nature, where so many disturbing factors come into play.   Ecological growth curves show irregularities just as do ecological assimilation curves.   The influence of water and of nutrient salts follows at lower concentrations a general "logarithmic" form; but at higher water contents and at higher concentrations of salts a maximum is reached and the curve begins to fall: other factors come into play.

The disturbing effect of higher concentrations of salts may well depend upon osmotic pressure; but their activity toward colloids, discussed at some length above, occurs at normal concentrations, and can exert a most profound effect upon growth.   This interaction of the purely chemical effect of the salts and their activity toward colloids is one of the most important problems for future research.

The action of nutritive salts upon plants in nature is, therefore, threefold.   First of all there is the purely chemical nutritive effect.   The salts are raw materials of the plant body;

and here the laws of Mitscherlich hold. Secondly, there is the osmotic effect which appears at high concentrations, and which causes a falling off in the growth rate. Thirdly, there is the colloidal effect of the ions; and the curve of growth determined by this influence may be periodic in shape. To more detailed consideration of the ecological effects of phases two and three, we shall return later. For the present attention will be confined to the simple chemical effect when two or more factors vary simultaneously.

TABLE XXXII

YIELD OF OATS AFTER MANURING WITH MONOBASIC CALCIUM PHOSPHATE

P_2O_5 in Manure in gm.	Yield in Dry Weight.		Difference.	P.E. of Difference.
	Observed.	Calculated.		
0·0	9·8±0·50	9·80	—0·39	—0·8
0·05	19·3±0·52	18·91	—0·56	—0·3
0·10	27·2±2·00	26·64	—2·37	—2·8
0·20	41·0±0·85	38·63	+3·22	+2·9
0·30	43·9±1·12	47·12	+2·49	+0·7
0·50	54·9±3·66	57·39	+6·64	+3·0
2·00	61·0±2·24	67·64	—	—

According to the original minimum law of Liebig, when several factors are acting upon a plant, the amount of growth is determined entirely by the minimum factor. Increasing factors other than the minimum factor should, according to Liebig, have no effect whatever upon growth. Experience has shown that this is not the case. All the factors making up the environment have an influence upon the growth, but only in proportion to their relative intensity.

Theoretically, the resultant action of several factors working in conjunction can be expressed by Mitscherlich's formula. If x, x_1, x_2, x_3,... denote the factors influencing growth, and c, c_1, c_2, c_3,... their respective constants, then, according to Baule, the formula can be written:

$$y = E \left(1 - e^{-cx}\right).\left(1 - e^{-c_1 x_1}\right).\left(1 - e^{-c_2 x_2}\right).\left(...\right)...$$

where E represents the highest absolute yield when all the factors are in maximum.

Mitscherlich's example is represented in Fig. 64, where two factors, x and z, vary. By the aid of this figure it is easy to understand the mutual action of the two factors. In Table
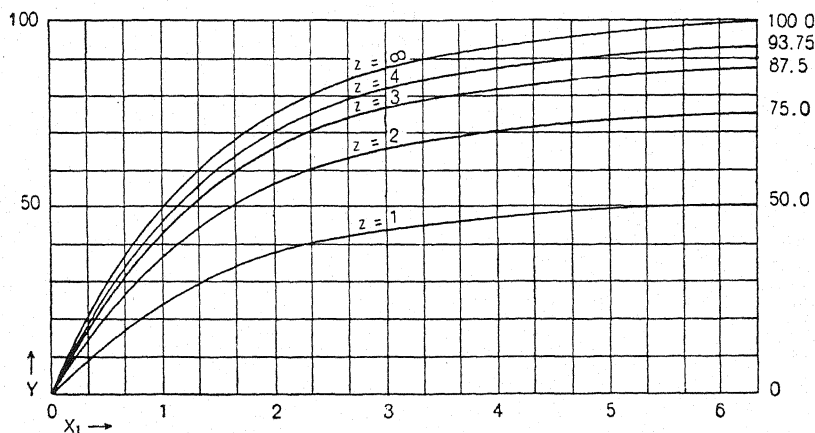
FIG. 64.—Graphical representation of the law of Relative Effects according to Mitscherlich's formula. The curves show the relationship between the yield Y and the factors x and z.

XXXIII are set out the relative and absolute effects of raising the factor x from 1 to 2, and of raising the factor y from 1 to 2, and to 4.

The relative effect of increasing one of the factors diminishes as its absolute value increases, but it is independent of the absolute value of the other factors.

TABLE XXXIII

THE RELATIVE AND ABSOLUTE INFLUENCE OF TWO GROWTH FACTORS

	$y=1$	$y=2$	$y=4$
$x=1$	25	37	46
$x=2$	40	60	73
Ratio	1·6	1·6	1·6
Difference	15	23	27
$x=3$	45	67	82
Ratio	1·1	1·1	1·1
Difference	5	7	9

There is still a dearth of experimental data to which the above formula could be applied. The work of Seelhorst and Tucker (1898), Mitscherlich (1916—1921), Russell (1927) and others, is no more than a preliminary survey of the field. There is no doubt, however, of the immense significance of the various aspects of the law of relative effects in agriculture and plant geography.

Agricultural research has repeatedly shown that excess or deficiency of a nutrient material will influence the morphological development of a crop (for details, the reader is referred to Kleberger, 1915; Schneidewind, 1921; Russell, 1927).

Excess of nitrogen favours vegetative growth, and delays ripening (Turner, 1922). The halms of cereals tend to lodge, and the general rigidity of the plant (the thickness of the cells and the amount of sclerenchyma) is reduced. Super-abundant nitrogen manuring seems also to facilitate the attacks of parasites, a state which is also obtained if the water supply is too abundant. The reason for this increased susceptibility is said to be the formation of collenchyma instead of sclerenchyma (Hursch, 1924).

The application of phosphates favours root formation and hastens maturity of fruit. According to Russell, the northern limit of grain cultivation can be extended still further northwards by abundant phosphate manuring. In Northern England the practice of applying phosphates to wheat is much favoured. A soil poor in phosphates is always unsatisfactory, for the quality and nutritive value of a crop depends largely upon adequate supply of phosphate. The developmental changes induced by phosphates are less evident than those following nitrogenous manuring (see Tottingham, 1914). Effects of phosphate starvation have been described by Henrici (1927), Ginsburg (1925) and Wallace (1925).

Potassium is concerned in the formation of chlorophyll, and appears to have some special rôle in the formation of starch. Plants which store up large quantities of starch or cane sugar, such as potatoes and sugar beets, are known as potassium plants. Deficiency in potassium lowers the resistance to fungal attack, and potassium manuring is recommended as the simplest method of minimizing risk of infectious plant diseases (Stakman and Aamodt, 1924). It is the common experience of farmers that sodium can replace potassium to some degree, but it cannot be said that one is a complete substitute for the other (Russell, 1927). Deficiency of potassium seems to upset the balance of the assimilation process, and brown flecks often appear on the leaves (Garner, 1923).

Calcium increases the rigidity of the plant, and stimulates the growth of root hairs (Hansteen, 1910; Lundegårdh, 1911). According to Hansteen, and Lillie (1923), the effect of calcium depends upon the fact that it precipitates certain substances

in the cell, especially the phosphatides and pectic materials. This precipitating action of calcium may be of great importance to the cell, for it would prevent the introduction of harmful and unnecessary substances into the cell, and it would reduce the loss of phosphatides.

It has long been known that plants exert a certain specificity in their choice of inorganic food materials. When different kinds of plants are grown in the same kind of culture solution the various ions are absorbed in very different proportions. The most striking example of this has been given by Oster-hout (1922) for the alga *Valonia*. *Valonia* contains in its cell sap a higher concentration of KCl and a lower concentration of NaCl than that of the surrounding sea water. The concentration of ions of magnesium, calcium, and sulphate also differs inside and outside the cell. The high potassium demand of beets, etc., has already been mentioned. Nitro-philous plants, which demand large amounts of nitrogen, thrive in woods and mould soils and among seaweeds, where there is vigorous nitrification (Holmgren, 1921). According to Hesselmann (1917), *Epilobium angustifolium* and *Rubus idaeus* are highly nitrophilous plants. Both can exist under extreme conditions of light and moisture, but they are com-pletely dependent upon nitrification in the soil. *Urtica dioica* is another nitrate-plant. Carsten-Olsen has determined the nitrate content of the soils in a number of different situa-tions where *Urtica* was more or less abundant (1921). His results are presented in an abridged form in Table XXXIV.

TABLE XXXIV

Development of *Urtica dioica*.	Nitrate Content of 1 litre Fresh Soil.
225 cm. high	107·9 mg.
200 ,, ...	225·85 ,,
160 ,, ...	79·78 ,,
100 ,, ...	50·04 ,,
80 ,, ...	40·98 ,,
Absent	37·19–1·37 ,,

It would seem that the supply of nitrogen is the deciding factor in the distribution of *Urtica*.

Designations such as "potassium plant," "nitrogen plant," and "salt plant," are ambiguous. When a plant is observed to absorb large quantities of a particular salt, and observed to grow only upon soils rich in that salt, it is plausible to con-

clude that the plant really needs large quantities of this salt
for its development.

But this is not the sole interpretation which can be put
upon the facts. For it is also reasonable to suppose that
these plants grow in such habitats because they can tolerate
large quantities of potassium nitrate, etc., and because they are
able to store it up in their tissues without suffering any harm.
Many halophytes, for instance, can live perfectly well without
salt, but, in contrast to other plants, they are able to thrive
with large amounts of salt in their tissues. The "preference"
of such plants for salt soils is purely a question of competition.
For *Salsola*, for example, this interpretation is undoubtedly the
right one. On the sea-shore *Salsola* is found only on sand or
stony beaches, where the vegetation is very open and competi-
tion poor; and, according to Clements, it occurs on the prairies
in situations which for some reason are destitute of other
vegetation (Clements, 1916). According to Kolkwitz (1917;
1918; 1919), halophytes are able to grow on gypsum soils.
Montfort (1926; 1927) has shown that salt from the sea
inhibits the assimilation of halophobes, and promotes the
hydrolysis of starch, whereas halophytes are not affected.
Poma (1922) and Montfort have established the interesting
fact that halophytes germinate best in fresh water; their
resistance to salt is to some extent an ontogenetic adapta-
tion, and, indeed, this resistance is only toward "balanced"
solutions.

Various hypotheses have been put forward to explain the
physical and chemical causes of succulence; these have been
fully discussed by Stocker (1928). Keller (1925) has demon-
strated that other salts beside sodium chloride can induce
succulence, though in very varying degree.

The distribution of various halophytes on the sea shore
may be explained by their specificity as to the optimum salt
concentration in the soil solution, though naturally other
factors will contribute to the zonation. Innumerable inves-
tigations have been published upon this subject. For details
and the bibliography of the subject the reader is referred to
Priestley (1911); Johnson and York (1912); Transeau (1913);
Hill and Hanley (1914); Yapp *et al.* (1916); Clements (1916,
p. 233). Yapp's system is represented graphically in Fig. 65.
Sernander (1917) has proposed the following classification of
the zones, more especially to be distinguished along a rocky
shore:

1. The littoral zone, which is beneath the average level of the water.

2. The lower supra-littoral zone (the "splash zone") ; the extent of which depends largely upon the exposure.   On the windward side of the island of Schären in the Baltic the zone is much wider than it is on the leeward side.   Phanerogams occur only in crevices in the rocks.   The dominant plant is *Verrucaria Maura*.

3. The upper supra-littoral zone, which is characterized by the lichens *Placodium murale* and *Xanthoria parietina*. Here are to be found, too, the facultative halophytes *Statice Armeria*, *Festuca rubra*, and *Sedum acre*, which increase rapidly

Associations	Salicornia	Glyceria	Armeria	Spergularia	Aster	Glaux	Triglochin	Plantago Maritima	Lepturus	Festuca	Agrostis	Plantago Coronopus	Juncus Gerardi	Cochlearia	Juncus Maritimus
5 Juncetum Maritimi															
4 Festucetum upper / lower															
3 Armerietum Maritimae															
Glycerietum Maritimae															
1 Salicornetum Europaeae															
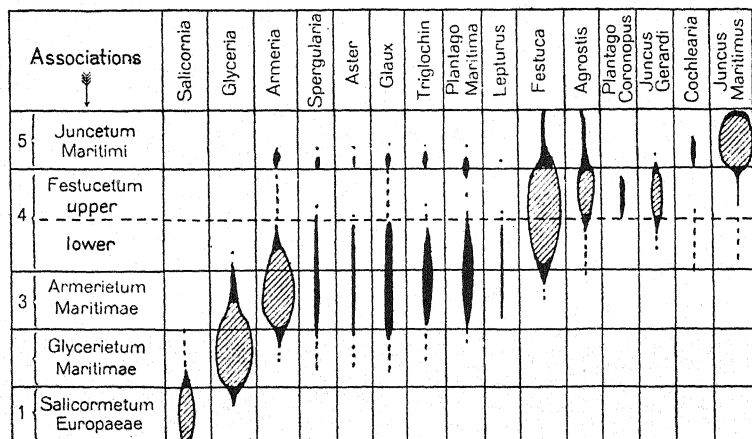
FIG. 65.—Diagram to illustrate the zonation of vegetation on a northern sea shore.   (Yapp *et al.*)

in numbers toward the upper boundary of the zone.   Monocotyledons such as *Juncus*, *Bromus* and *Agrostis* also occur.

4. The epilittoral zone which extends to the edge of the non-halophytic land vegetation; the flora is a "beach scrub," *Prunus spinosa*, *Cotoneaster*, and species of *Rubus* and *Rosa*.

As has already been emphasized, the zonation is not due alone to a decreasing salt concentration; the zones nearer the sea have a higher water content and a lower aeration.   The characteristic flora of recent beds of seaweed is a mixture of swamp plants and halophytes (Holmgren, 1921).

In dealing with the flora of a sea shore account must also be taken of the movement of the soil and erosion.   Only those plants with a well-anchored root system and hardy leaves are able to establish themselves.   A plant like *Atriplex*, which

roots on the surface, is only to be found in the lower zones, in quiet bays.

In successive zones from the sea to the land, the salt content diminishes rapidly. On a flat exposed rocky beach, after a long drought, the author found the salt concentration of the *Placodium* zone to be no more than 0·045–0·153 per cent. This roughly corresponds to the normal concentration of a nutrient solution. In the middle of a reef about three metres high, and ten metres from the sea, the salt concentration of the soil solution, after a drought in July, ranged from 0·033–0·2 per cent. On this reef there had developed an assortment of pseudo-halophytes (*Matricaria maritima*, *Atriplex litoralis*, etc.) and mesophytes such as *Alopecurus geniculatus*, *Malva rotundifolia* and *Poa pratensis*.

Halophytes possess certain adaptations which restrict the absorption of salts, so that their permeability for pure sodium chloride is very low. In certain exceptional instances there is an active excretion of salt through the hydathodes (Lundegårdh, 1919).

It is remarkable that the halophytes are so little specialized to definite salts; they can flourish in the presence of large quantities of sulphates, magnesium and calcium, and even of hydroxyl ions. The imbibition of the protoplasm, which is so markedly influenced by ions, must vary widely in these plants without harming them at all. It is not well known how the more nearly normal plants behave in this respect. Perhaps their "antipathy" toward higher concentrations of salts can be attributed to a more sensitive state of imbibition of the protoplasm (Walter, 1923).

There are also some plants which are adapted to higher concentrations of various other "unnecessary" salts. *Viola calaminaria* and *Alsine verna*, for instance, grow luxuriantly in soils containing a high percentage of zinc, and the ash content of the plants may contain as much as 13 per cent of zinc. (Schimper, 1897.)

As regards their reaction to the mineral content of the soil, plants can be divided into four groups. To the first group belong the so-called oligotrophytes, plants which grow on soils poor in salts, and on dunes and highly acid soils. The second group comprises the eutrophic plants, which inhabit meadows and woodlands; and in the third group are classed plants which are specialized to certain salts: the nitrate plants and the zinc plants. Finally, in the fourth group, come the halo-

phytes.   The distinction of the last two groups is somewhat arbitrary; indeed there are many nitrogen plants which could be classed as facultative halophytes, as, for example, species of *Atriplex*, *Rumex crispus* and *R. maritima*, *Potentilla anserina*, etc.

Such a classification of plants according to their salt require-ments gives some idea of the significance of the salt content of the soil in plant geography.   In an area of uniform climate, it is fairly easy to reconcile the distribution of species with the relative content of nutritive salts in the soil.   This, how-ever, does not prove conclusively that the supply of mineral salts is in every case the deciding factor, for the physical constitution of a soil poor in mineral salts differs markedly from that in a richer soil.

The plant inhabitants of soils poor in mineral salts always grow slowly.   Massart (1918) noted this for dune plants; and the slow growth of *Calluna* and other heath plants is well known.   Their slow growth is somewhat specific to these plants, for even in soils rich in nutrients, they do not grow very fast.

Sphagnum is commonly taken as an example of a "salt-shy" plant.   Skene has shown, in culture experiments, that the optimum growth of *Sphagnum* occurs at lower concentrations than are optimal for other plants, especially when the reaction of the medium is alkaline.   (*See* Table XXXV.)

TABLE XXXV

THE GROWTH OF *SPHAGNUM* IN NUTRIENT SOLUTIONS.   (Skene, 1915.)

Concentration in Percentages.	Growth in Percentages.	
	Acid.	Alkaline.
0·01	66	63
0·05	76	43
0·1	73	20
0·25	51	33
0·5	35	27

The salt concentration in lakes and rivers varies from 0·1 to 0·5 per cent, and this concentration of culture solution is generally to be recommended for eutrophytes.   According to Hoagland and Sharp (1918), the concentration of the soil solution in a moderately damp cultivated field varies from 0·1 to 1·0 per cent.   Eutrophytes are very sensitive to this concentration of soil solution, as the figures of Hoagland and Sharp in Table XXXVI show.

TABLE XXXVI

GROWTH OF RYE IN CULTURE SOLUTIONS. (Hoagland and Sharp.)

Concentration of Solution in per cent.	Dry Weight of Green Part of Plants.	Uptake of Salts per Culture, per cent.
0·02	0·43 gm.	0·0025
0·08	0·46 „	0·0072
0·25	0·50 „	0·0288
0·60	0·50 „	0·0402

Halophytes, on the other hand, will grow excellently in concentrations of 2 per cent. According to Halkett (1926), the optimum concentration of sodium chloride for the growth of *Salicornia* is from 2 to 3 per cent; and growth takes place at concentrations as high as 17 per cent.

Waynick (1918) found that the use of unbalanced solutions often resulted in an inundation of the plant tissues with magnesium and other salts, and a concomitant decrease in the growth rate. The decrease in the growth rate may be due to a reduction in the degree of hydration of the protoplasm, brought about by an excess of free ions. The choice of an adequately balanced culture solution for experimental work, therefore, is of the greatest importance. There is an additional complication due to the fact that the antagonism changes with different concentrations of the solution.

The physical constitution of the soil is an important factor in determining the salt concentration. In a soil of high adsorptive power the concentration of the soil solution remains more nearly constant than in a soil like a sand, in which the adsorptive power is low. The adsorptive power of the soil colloids enables them to act as a kind of buffer.

The effect upon crops of changes in the concentration of the nutrient solution is a subject which has received considerable attention; for the experiments in this field, reference may be made to Hall and Russell (1912); Stiles (1915); Breazeale (1905); and Burd (1919). Pearsall (1924) attributes the periodicity of plankton to variations in the oxygen and salt content of water. Systematic experiments have been carried out by several American investigators (Tottingham, 1914; Shive, 1915; Livingston and Tottingham, 1917; and Dickson, 1921).

It is clear that among different plants there is an extraordinary range of specialization as regards the optimum concentration of the culture solution in which they grow. With most plants, several combinations will give optimum growth.

In nature, the effect of salt concentration is bound up with many other factors—the temperature, the water content of the soil, and the competition among the plants themselves.

2. CHALK PLANTS [1]

In many respects calcium occupies a peculiar position among inorganic nutrients. On account of their activity toward colloids, calcium ions are indispensable to a balanced nutrient solution; they regulate the hydrogen ion concentration of the soil and of water; and they promote the formation of a neutral humus, and the activity of micro-organisms in the soil. Moreover, calcium carbonate regulates the p_H of the soil.

For a century it has been known that certain plants grow exclusively upon chalky soils; and that other plants avoid chalk (Wahlenberg, 1814; Unger, 1836). There are certain lower plants which can grow in solutions free from calcium; and even for the distribution of these plants in nature calcium plays some part, for it reduces the poisonous effect of hydrogen ions (Lundegårdh, 1924, b). *Sphagnum* is always quoted as a very strong calciphobe; Paul (1906) has shown, however, that it is specifically calcium carbonate which is toxic, for *Sphagnum* is not sensitive to gypsum. Mevius (1924) has shown that *Sphagnum* will stand quite high concentrations of salts, even of calcium, if the medium is sufficiently acid; it is apparently the [OH] ions which are poisonous. The similar behaviour of other mosses, *Polytrichum commune*, for instance, can also be explained on the assumption that their maximum growth occurs in a somewhat acid medium. According to Boas, *Polytrichum* thrives best in a concentration of 0·002 per cent of sulphuric acid.

Among the phanerogams there are very few real calciphobes. Plants such as *Sarothamnus scoparius*, *Pinus pinaster*, and *Castanea vesca* carefully shun soils containing more than a few per cent of chalk, though, like all the higher plants, they cannot live entirely without calcium. Mevius seems to have established that the calciphobe nature of *Sarothamnus* and *Pinus pinaster* depends upon the fact that they will not grow in neutral or alkaline soils. Mevius is of opinion that the roots of these plants have a very low power of decom-

[1] For recent work on this subject the reader is referred to Zollitsch (1927), Mevius (1927), Pesola (1928) and Braun-Blanquet (1928).

position, and that in a neutral soil they are unable to absorb the necessary iron from the ground.

It has long been known that calciphobus plants, when cultivated in a soil containing calcium, tend to become chlorotic. This can easily be explained on the assumption that, under the influence of calcium ions, the plasma membrane is impermeable to ferric ions. (For a survey of the literature, *see* the work of Carsten-Olsen, 1921). The absorption of potassium ions is also inhibited (Fliche and Grandeau, 1874; Büsgen, 1914; Gile and Carrero, 1920). Some of the so-called calciphobes are "potassium plants" which cannot absorb sufficient potassium on a chalky soil (Salisbury, 1920). According to Engler (1901), the calciphobous plant *Castanea* will thrive on chalky sandstones and marls, if these are sufficiently rich in potassium.

It is not known with any certainty whether the inhibitory effect of calcium upon the absorption of other ions is a purely colloidal phenomenon, for calcium affects various other properties in the soil. According to Ehrenberg (1920), chalk increases the solvent action of the soil acids for other rocks. It is noteworthy that in some experiments with wheat seedlings, Lundegårdh and Morávek observed that calcium in concentrations of $N/100$ to $N/400$ did not affect the uptake of nitrates, phosphates and potassium (1924). Maquenne and Demoussy report the interesting fact that calcium does not inhibit the permeability of the plant in the presence of copper (1920).

The behaviour of the true lime plants is bound up with the physical properties of the soil, and the climate in which the plants are growing. Thurmann, as long ago as 1849, remarked that a number of plants (*Clematis vitalba, Buxus sempervirens, Teucrium chamaedrys,* and *Helleborus foetidus*) which occur on the chalk in Northern France, appear in the Cevennes on gneiss. Brenchley (1912) mentions that weeds which are calciphobes in Eastern England, grow on chalk in the west. Hall and Russell (1911) are of opinion that the productivity of chalk soils depends to a high degree upon the prevailing moisture and temperature conditions. This influence of climate upon the reaction of plants to lime in the soil would indicate that the reaction is largely dependent upon the physical condition of the soil.

Kraus, in his monograph (1911), has laid great stress upon the significance of the soil structure in studying the

distribution of plants on chalk soils.   In the limestone of the
Maine valley Kraus found a number of genuine chalk plants
which grew only on soil where sufficient chalk was present.
Beside these, however, there were perfectly clear cases of well-
recognized chalk plants, such as *Pulsatilla* and *Hippocrepis
comosa*, growing on siliceous soil almost free from chalk; but
they were only to be found where the physical constitution
of the siliceous soil, its temperature and water content, were
similar to those of the chalk.   In contrast to this, Kraus found
typical calciphobes, *Calluna vulgaris* and *Vaccinium myrtillus*,
growing on soils which contained 3·4 per cent of chalk.   In
Table XXXVII are recorded some of the observations of
Kraus.

TABLE XXXVII

Obligate Chalk Plants.	Facultative Chalk Plants.	Calciphobus Plants.
Libanotis montana 9·0–37·7% *Linosyris vulgaris* 5·7–5·8% *Aster amellus* 4·5–27·5% *Bupleureum falcatum* 3·0% *Helianthemum poly-folium* 3·1%	*Cytisus nigricans* 0·0–27·5% *Cervaria rigida* 0·0–68·6% *Hippocrepis comosa* 0·0–68·6% *Anthemis tinctoria* 0·0–32·4% *Vulneraria* 0·0–6·2% *Pulsatilla* 0·0–53·6% *Inula hirta* 0·0–1·7% *Galium glaucum* 0·0–5·9% *Alyssum montanum* 0·0–4·0%	*Teucrium scorodonia* 0·0–4·2% *Calluna and Vaccinium* 0·0–3·4% *Sarothamnus scoparius* 0·0%

The percentages refer to the calcium content of the soil around the roots.

Still another difference between chalk soils and siliceous
soils is the abundant bacterial life in the chalk, which results
in a more abundant formation of nitrates and organic nitrogen
compounds.   Bear (1917) and various other investigators
have declared that the chalk plants are "nitrate plants," while
those growing on siliceous soils prefer their nitrogen in the

form of ammonia. A more recent investigation of Olsen, however, does not confirm this view (Olsen, 1921). Olsen is of opinion that ammonium and nitrate have the same value as sources of nitrogen, for both calciphilous and calciphobous plants. Mention might finally be made of the hypothesis put forward by Truog (1918) and other authors, namely, that the "chalk plants" are plants which really do need a large proportion of calcium in their tissues. For details of this view, the reader is referred to Truog's paper.

On account of its solubility, chalk is gradually washed out of the upper layers of the soil. The unfertilized fields at Rothamstead have lost 50 per cent of their chalk content in a century (Hall, 1921). Even when the geological substratum is rich in chalk, the friable soil in which the roots develop may be very poor in calcium. As the investigations of Kraus have illustrated so well, nothing short of a chemical investigation of the soil immediately around the roots will reveal the true calcium content of the soil. Statements by the earlier writers about the distribution of chalk plants have to be accepted, therefore, with great reservations.

In summarizing modern ideas concerning chalk plants, it can be emphasized that very few plants are consistent in their reaction toward calcium. Most chalk plants flourish on chalky soils, not because they need large quantities of calcium as a nutrient, but on account of the physical structure of the soil, its general richness, and its neutral or alkaline reaction. When these subsidiary characters of a chalk soil are found, in the absence of large quantities of calcium, the so-called facultative chalk plants grow perfectly well.

One other example of such facultative chalk plants is of interest. *Quercus sessiliflora* and *Fagus sylvatica* flourish on soils rich in lime, but when the climate and physical conditions of the soil are favourable, these trees will develop excellently on soils poor in calcium (Tansley, 1911). The demand made upon the soil changes to some extent with the ontogenetic development of the plant; juvenile forms of *Pinus sylvestris* are more sensitive to an acid reaction than trees two to three years old (Salisbury, 1920). Nägeli's classical example of *Achillea atrata* and *Achillea moschata*, said to illustrate the interference of competition in the distribution of facultative chalk plants, is not, according to the work of Zollitsch, to be attributed to their reaction to chalk, but to the degree of acidity in the soil.

In general, the plants classed as calciphobes do not avoid the calcium ion as such, but cannot endure the alkaline reaction which accompanies it, or the change in permeability which the calcium ion produces. In many instances, such as the disease in oats, due to manganese deficiency, it has not yet been determined which of these factors dominates the situation. It has often been assumed that this disease in oats is due to an upsetting of the ion-balance, brought about by an excess of calcium. Recent work in the writer's laboratory has shown, however, that the disease occurs when $CaCO_3$ is used, but does not occur when $CaCl_2$ is used. Several ions [Mn] and [NH$_4$] will prevent the disease, and [NO$_3$] will encourage it. It is quite clear that the influence of chalk on vegetation is much more complex than has hitherto been recognized, and that it depends upon other ions present in the soil.

The effects of chalk on vegetation, therefore, are manifold, and have induced a whole series of physiological life forms. Through its influence upon water content, alkalinity and the bacterial activity, chalk occupies a most interesting place among the chemical factors in the soil.

3. Hydrogen Ion Concentration [1]

A great many calciphilous and calciphobous plants react not so much to the calcium ions in the soil, as to the hydrogen and hydroxyl ions. *Sphagnum* has already been cited as an example of such a plant. Within the last few years the hydrogen ion factor has been in the limelight of research and there exists already an extensive literature on the subject.

The soil contains some free hydrogen ions, and others loosely combined as acids. The free ions constitute the "hydrogen ion concentration" and the others the buffer substances, which regulate the concentration of the hydrogen ions. The physiological action of the free hydrogen ions is considerable, for even the smallest changes in the concentration may have a critical effect. The influence of the buffer substances is more indirect, and attains significance when a soil is exposed to influences which tend to change the hydrogen ion concentration. It is, therefore, very important to distin-

[1] The extensive literature on this subject has been summarized by Arrhenius (1926), Mevius (1927) and Kappen (1929), so that no exhaustive treatment has been attempted here.

guish between the free and the combined hydrogen ions, and to determine them separately.

The determination of the hydrogen ion concentration was greatly facilitated by the introduction of a colorimetric method. For the details and theory of this method, the reader is referred to Clark (1922), Sörensen (1909) and Michaelis (1922). Recently, however, the electrical method, which is theoretically the most satisfactory, has been so improved that a determination can be carried out in a few minutes. The quinhydrone apparatus, which does not need a stream of hydrogen, can now be obtained in portable form.

The absolute hydrogen ion concentration of a soil is very small indeed, and is more conveniently expressed in terms of a reaction number, the p_H value. This value is the negative logarithm of the normality of hydrogen ions. A normality of $N/10^7$ is the neutral point, and is denoted by p_H 7·0. Values below 7 represent an acid reaction, and values above 7 alkaline reaction.

The p_H value of the soil varies between about 3 and 11. In America soils as acid as 1·7 have been recorded (Arrhenius, 1922) and in Egypt soils as alkaline as 11. Chalk soils are never more alkaline than 8·4, while magnesium carbonate can bring the p_H up to 10.

In determining the p_H value of a soil, the procedure is to shake a small quantity of soil with four times its volume of water. After a few minutes the extract acquires the same hydrogen ion concentration as the soil solution itself. In nature the rain-water is rapidly brought to the same p_H as the soil on which it falls. When the hydrogen ions are neutralized through the introduction of a base into the soil, the buffer substances liberate a new charge of ions, and this supply will continue until the buffer substances are quite used up. Thus the amount of base necessary to neutralize a soil has to be equivalent to the amount of buffer in that soil, and the relationship is similar for alkaline soils.

The total amount of buffer is determined by titrating the soil to the neutral point. Up to the present the nature of the buffers is unknown; they probably include some of the humus materials and inorganic components like the zeolites (H. W. Johnson, 1922). There is no doubt that the buffering is effected by several substances, and that it is brought about in various ways; so that one would expect the neutraliz-

ation of the soil to take place in a number of stages.   The general *shape* of the neutralization curve is determined by titration in the following manner:

A soil sample is divided into a number of equal parts, and these are covered with varying quantities of N/100 sodium hydroxide or hydrochloric acid.   After twenty-four hours the
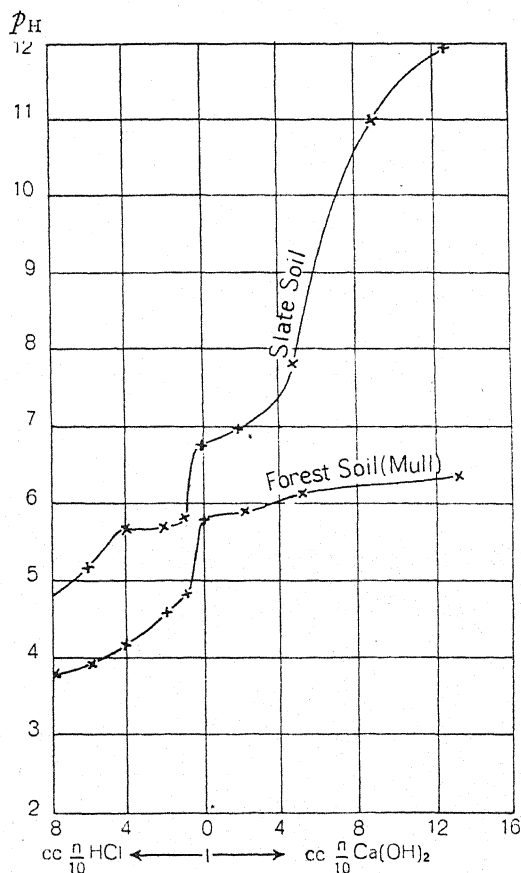
FIG. 66.—The titration curves of two Norwegian soils.   (Gaarder and Hagem, 1921.)

p_H values of the mixtures are determined.   Results of this sort, obtained by Gaarder and Hagem, are represented in Figure 66; from such a graph the buffer action at any value . of the p_H can be read immediately.   (*See* Bjerrum and Gjald-baek, 1919; Gaarder and Hagem, 1921; Tovborg-Jensen, 1924).   Work in this field, up to the present, has been directed toward the effect of the actual p_H upon plant growth.

Owing to the difficulties in the technique of estimating p_H, too much reliance cannot be placed upon the results so far obtained; and it is not possible to make any final statement as to the significance of hydrogen ion concentration in the distribution of vegetation.

That there is a parallelism between the distribution of plants in nature and the hydrogen ion concentration has been shown by a number of investigators (Hoagland, 1917; 1918; 1919; Wherry, 1920; Gillespie, 1920; van Alstine, 1920; Arrhenius, 1920; 1922; Olsen, 1921; Salisbury, 1920; Kappen, 1916; 1920; König, 1922; Kurz, 1923, and Braun-Blanquet, 1928). The most comprehensive of these contri-

| p_H | 3 | 4 | 5 | 6 | 7 | 8 |

——————— Deschampsia flexuosa — — — — Senecio silvaticus
—·——·— Tussilago farfara ············ Hordeum distichum
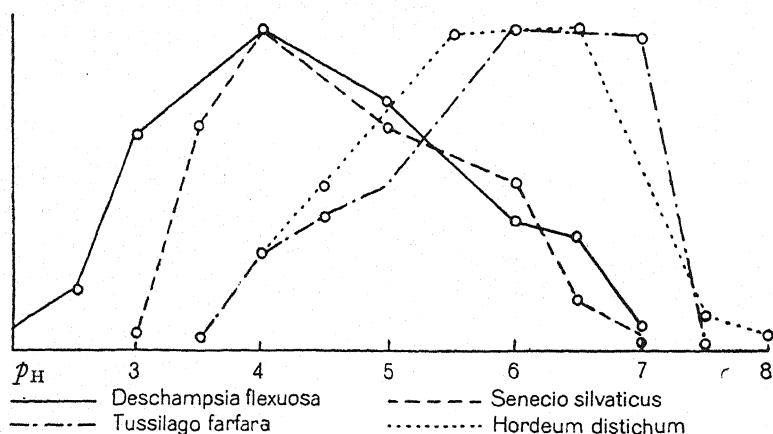
FIG. 67.—p_H curves of the growth of four species of plants in culture solution. (Olsen, 1921.)

butions is that of Olsen, who observed the frequency of a number of species in 76 different habitats, and was able to determine the optimum p_H value for the distribution of each species. The results showed that most plants were able to flourish in a very wide range of p_H values, though generally a definite optimum could be distinguished. The effect of hydrogen ion concentration was more marked in artificial culture, either in soil or solution, than in nature (Fig. 67). In Table XXXVIII are given some of Olsen's results.

Experiments in artificial culture often give a twofold optimum for the p_H (Hixon, 1921; Hopkins, 1922; O. Arrhenius, 1922; Lundegårdh, 1923, c; Theron, 1924). In ecological studies there does not always exist a well-defined optimum hydrogen ion concentration, but the investigations

TABLE XXXVIII

THE RELATIVE FREQUENCY OF MEADOW PLANTS IN CLASSES OF p_H

p_H Classes	3·5–3·9	4·0–4·4	4·5–4·9	5·0–5·4	5·5–5·9	6·0–6·4	6·5–6·9	7·0–7·4	7·5–7·9
Deschampsia flexuosa	86	68	40	—	—	—	—	—	—
Molinia coerulea	94	84	46	13	0	50	40	30	—
Calluna vulgaris	20	47	10	20	—	—	—	—	—
Carex Goudenoughii	30	70	100	55	90	65	74	65	42
Festuca rubra	—	37	43	71	99	86	96	86	100
Ranunculus acris	—	—	13	53	62	58	51	90	63
Deschampsia caespitosa	—	—	—	40	67	62	33	52	23
Festuca elatior	—	—	—	—	25	70	61	87	73
Tussilago farfara	—	—	—	—	—	10	10	55	80

TABLE XXXIX

THE RELATIVE FREQUENCY OF WOODLAND PLANTS IN CLASSES OF p_H

p_H Classes	3·5–3·9	4·0–4·4	4·5–4·9	5·0–5·4	5·5–5·9	6·0–6·4	6·5–6·9	7·0–7·4	7·5–7·9
Vaccinium myrtillus	100	—	—	—	—	—	—	—	—
Convallaria majalis	100	68	—	—	—	—	—	—	10
Oxalis acetosella	20	62	74	76	78	61	65	54	43
Anemone nemorosa	10	61	88	76	77	91	94	95	65
Mercurialis perennis	—	—	30	70	87	81	80	80	87
Allium ursinum	—	—	—	—	100	85	100	100	100
Anemone hepatica	—	—	15	15	15	10	25	59	63

The frequencies were determined by Raunkiaer's quadrat method, and are expressed by percentages.

leave no doubt whatever that the hydrogen ion concentration is a most important factor in the habitat. It is evident from Figure 67 that if a mixture of seeds of *Deschampsia flexuosa, Senecio sylvaticus, Tussilago farfara,* and *Hordeum disticum* is sown in soils of p_H 4 and p_H 6, two entirely different populations will arise. The p_H curves of crop plants, too, vary widely, a fact which is of considerable importance in Agriculture. Not only is the optimum p_H specific for different species, but even for different strains of the same species (Arrhenius, 1925; Stark, 1928).

Work of the present writer (1923, *c*; 1924, *c*) and others (Salter and McIlvane, 1920; O. Arrhenius, 1922) has

demonstrated an influence of p_H upon germination. The percentage germination of seeds at different values of the p_H is shown in Figure 68. The growth of bacteria, fungi, fresh water and marine algæ all depend to a great extent upon the p_H value.

It has been observed in the realm of plant pathology that host plant and parasite grow within different ranges of hydrogen ion concentration. The parasite in potato scab, *Actinomyces scabies*, is killed at a p_H of 5·0—5·2, so that the increase of hydrogen ion concentration by the addition of sulphur to the soil effectively controls this disease (Waksman, 1922; Gillespie, 1918; Hopkins, 1922; Lipman, 1919). Heart rot of beets cannot occur at a p_H less than 6·7, while root rot occurs only in acid soils. In symbiosis, on the other hand, it is important that the p_H should be at an optimum common to both symbionts. The formation of nodules on soy beans occurs best, according to Bryan (1922), at a p_H of 6·5, and the limits within which nodule formation will take place are p_H 3·6 to 8·0.

FIG. 68.—The p_H curve of the germination of wheat. (Lundegårdh, 1923.)

The hydrogen ion concentration plays a part, too, in the velocity and the course of decomposition in the soil. The very careful investigations of Christensen (1914; 1923) have shown that the distribution of *Azotobacter* is so limited by p_H that its occurrence on infected soils is a reliable test of the reaction of the soil, and of the soil's lime requirement. Below a p_H of 5·8 *Azotobacter* disappears altogether; and as the figure shows, its development decreases rapidly below a p_H of about 6·6. (Fig. 69.) The nitrifying bacteria, on the other hand, seem to flourish in acid soils (Blair and Prince, 1922; and references in their paper). There seems to be no justification for the earlier view, that nitrification takes place principally on neutral soils. Of the limits of p_H of individual fungi in the soil nothing of any certainty is known;

the original idea, that fungi occur in acid soils, appears on the whole to be correct (Waksman, 1922; 1924).

In spite of the enormous literature concerning hydrogen ion concentration as a soil factor, there is still great uncertainty over the most fundamental problems. We know next to nothing of the manner in which hydrogen ions affect plants. It has been suggested that the ions alter the charge of the plasma colloids, and thereby alter the permeability for salts. A high hydrogen ion concentration causes a decrease in the absorption of potassium and calcium (Gordon and Starkey, 1922); the uptake of iron, too, is dependent upon the hydrogen ion concentration (van Alstine, 1920). Arrhenius is of the opinion that at the optimum p_H, the permeability is at a mini-
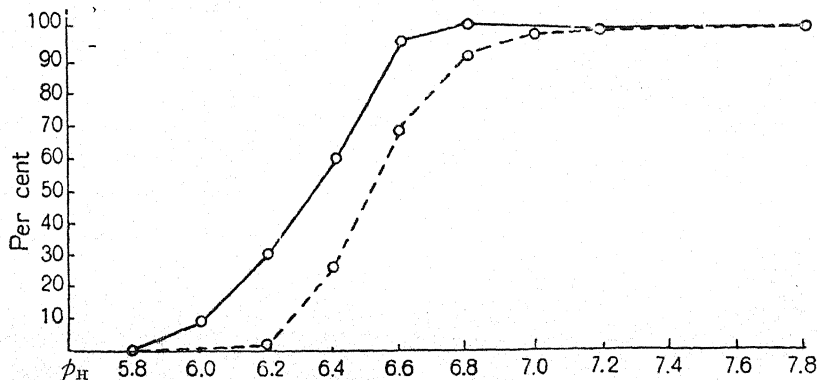
FIG. 69.—The growth of *Azotobacter* in soils of different p_H. The continuous curve represents the growth with smaller quantities of *Azotobacter*; the dotted curve represents the growth when large numbers are present. (Christensen.)

mum, and that at the limits of the p_H curve the permeability is higher (1922). There is great need at present for a thorough investigation of this problem.

The ecological effect of hydrogen ions may depend partly upon their influence on certain properties of the soil; they are very active toward colloids, and they determine the degree of dispersion of clay and humus, and the solubility of certain of the mineral constituents. The chlorosis of soy beans growing in a soil with p_H value greater than 5·0, may be associated with the precipitation of ferric phosphate at or about the neutral point. The reaction of the soil is of great importance for the solubility of aluminium compounds, for in acid soils aluminium goes into solution. A number of American workers are of opinion that the harmful effect of

acid soils is really due to the influence of aluminium (Mirasol, 1920; McIntire, 1921; Blair and Prince, 1923; Burgess, 1923; Conner and Sears, 1922). This view still merits some consideration, despite some contradictory experiments (Olsen, 1921).

Finally, some consideration must be given to the indirect effect of hydrogen ions upon the micro-flora of the soil. With the exception of some work on *Azotobacter* we have no reliable data on this subject. The production of nitrogen by *Azotobacter* is greatly reduced in acid soils, though whether this would be true of other nitrogen-fixing bacteria, we do not know. The micro-flora of the soil is amazingly rich in forms and species; many of them, though their metabolism differs widely, perform the same function in the soil, so that the transition from one concentration of hydrogen ion to another, in the course of the soil's development, is an imperceptible process. The course of development of a soil—its evolution—is so bound up with the nature of the micro-flora, the atmosphere, the climatic factors, that it is well-nigh impossible to decide what part is played in the development by the hydrogen ion concentration. It may sometimes be more accurate to regard the hydrogen ion concentration as an *effect*, an indicator of the development of the soil.

As has already been mentioned, it is the rainfall and the drainage of the soil which determine the nature of the soil reaction. The leaching out of the salts which occurs in a damp climate causes a mineral soil to develop an acid reaction (H. W. Johnson, 1922). Salisbury (1922) found that the oldest dunes on the sea shore have a p_H of 6·24, while the p_H value of more recent dunes was 7·8. Several substances are washed out, calcium carbonate, potassium, magnesium, etc., while phosphates tend to remain behind. (*See* the analyses of Hilgard, 1906.)

The leaching out is most severe in the superficial layers of the soil; accordingly the p_H increases with the depth. A further cause of low p_H at the surface is the higher humus content there. (Table XL, from Salisbury.)

This condition occurs, of course, only in a soil initially rich in calcium, and from which regular leaching out has taken place. Weiss (1924) found a very acid reaction in the upper layers of a beechwood soil in Denmark; samples taken from beneath the surface were less acid, and sometimes even neutral.

TABLE XL

LEACHING OUT FROM THE SOIL ON A DUNE

	Ins. below Surface.	Carbonate in per cent.	p_H.
Summit of hill	0–4	0·00–0·02	5·1–5·4
(*Pteris* dominant)	2–4	0·01–0·04	5·3–6·0
Half-way down	0–1	0·68–1·00	7·3
(chalk meadow)	2–4	1·1–3·2	7·3–7·4
Foot of hill	0–1	2·1–3·0	7·4–7·6
(chalk meadow)	2–4	25–65	7·6
Soil of a dry valley, chalk	0–1	12·5	7·5
meadow with bushes	2–4	20	7·5

Braun-Blanquet has obtained similar results from Alpine humus soils. If the sub-soil is rich in chalk there is generally a sharp change in p_H between the humus layer and the mineral soil beneath. In the neutral red earth soils in the Mediterranean region, on the other hand, there seems to be an increase of the concentration of hydrogen ions with the depth. This may well be due to the more arid character of the soil, since there will be an accumulation of salts in the upper layers.

Closely correlated with these changes in the composition and hydrogen ion concentration of the soil there occur changes in the vegetation. According to Salisbury, the evolution of a woodland soil in England takes place on the whole in the direction of a lower p_H. A genuine neutral mould soil, however, can be maintained in good condition so long as the calcium content does not fall below a certain level. Plants are always drawing up fresh supplies of calcium from the lower levels of the soil. This is stored in leaves and stems, and returns to the upper layers of the soil when the leaves and stems decay. For this reason deciduous trees are useful agents in maintaining a constant hydrogen ion concentration at the surface of the soil (Braun-Blanquet, 1928).

Investigations up to the present on the ecological effect of hydrogen ion concentration have suffered from one serious fault, namely, that this one factor has been singled out and regarded from too restricted a standpoint. The hydrogen

TABLE XLI

THE CHANGE IN p_H IN NORTHERN AND ALPINE PODSOLS. (Braun-Blanquet, 1928.)

	Acid humus Horizon.		Leached Horizon.		Horizon of Accumulation.		"Weathered" Soil.	
	p_H.	Depth cm.	p_H.	Depth cm.	p_H.	Depth cm.	p_H.	Depth cm.
Carex curvula assn. on rendzina podsol. (Central Alps) . .	5·0	0–0·5	5·7	35–38	6·5	38–45	7·8	45
Carex curvula assn. on humus podsol. (Central Alps) . .	5·5	0–3	5·4	3–13	5·4	13–18	6·3	18
Empetrum-Vaccinium uliginosum moor. (Central Alps) . .	4·2	2–5	5·0	15	—	—	—	—
Mixed *Larix-Pinus* forest. (Central Alps) . .	6·0	0–15	6·4	15–30	6·8	30–50	7·2	55
Calluna-Cladonia moor. (Norway) . .	4·3	—	4·4	—	4·7	—	—	—
Vaccinium myrtillus Betula pubescens forest. (Norway) . . .	4·0	—	4·0	—	4·7	—	—	—

TABLE XLII

CHANGE IN p_H IN MEDITERRANEAN RED EARTH SOILS. (Braun-Blanquet, 1928.)

	Horizon poor in humus.		Horizon stained red by iron and aluminium.		Raw weathered soil.	
	p_H.	Depth cm.	p_H.	Depth cm.	p_H.	Depth cm.
Brachypodietum ramosi on Jura chalk. (Montpelier) . .	6·8	1–5	6·5–6·5	15–60	—	—
Quercus ilex, young forest on Urgon chalk. (Pont-du-Gard) . . .	7·4	1–2	7·3–7·2	5–25	7·2	50
Quercus ilex bushes with Calluna on lime-free silicate . .	6·9	1–2	6·6–6·3	10–25	6·2	40–50
Quercus ilex forest (climax) in Atlas, overlying volcanic material (4,000 ft.) . .	7·2	2	7·2	10	—	—
Very open stand of *Quercus suber* on lime-free pleiocene sand. (Kenitra, Morocco) . .	7·2	2	7·0	10	6·9	30

ion concentration is undoubtedly an important factor in the habitat, but there is no justification for the assumption that it dominates all the other soil factors.   It has already been shown that the curve of p_H and growth often has a very indeterminate "flat" optimal region, and that normally growth can take place within a very wide range of p_H.   It may be assumed, though there are no data in support of it, that the hydrogen ion factor obeys the law of relative effects in growth, so that in the region of its optimum it would not exert a very marked effect on the vegetation.

Hydrogen ions act vigorously toward colloids.   It is
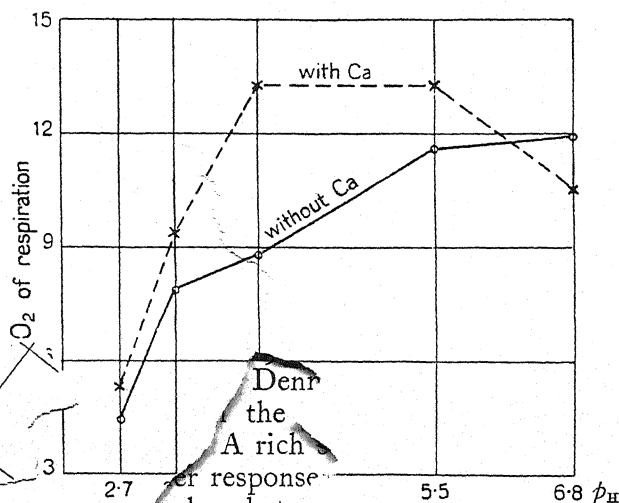
FIG. 70.—The develop... phosphat... *la Saubinetii* in peptone solutions of different p_H.   The broken c... portance... favourable influence of an addition of 0·05 per cent $CaCl_2$ to the ... The evolution of carbon dioxide of respiration was taken as a m... it is a... the growth of the fungus.   (Lundegårdh, 1924, *b*.)

therefore to be expected that hydrogen ions will exhibit some antagonism toward other colloidally active ions as regards their physiological influence.   This assumption has been justified by the independent investigations of Prianischnikow (1923) and of present writer (1924, *b*, *c*).   The graphs in Figure 70 show how the addition of calcium will remove the toxicity of hydrogen ions.   Prianischnikow investigated the resistance of cells to plasmolysis by acids, and he found, as Brenner had already found (1920), that the resistance was greater in the presence of calcium.

Still more important from the ecological standpoint are experiments with plants in culture solutions or in soils of

different p_H values, with and without calcium. The present writer investigated the growth of wheat seedlings in the soil on a large scale. A range of hydrogen ion concentrations was prepared by adding different quantities of hydrochloric acid to the soil. A series of control experiments without calcium, and series with 0·5 cc. and 5·0 cc. respectively of N/10 $CaCl_2$ per 50 gm. soil were replicated ten times. The results of the experiment are set out in Table XLIII.

TABLE XLIII

p_H.	6·8	6·1	5·5	5·2	4·4
Control	100	63	44	22	18
0·5 cc. $CaCl_2$	89	100	72	67	29
5·0 cc. ,, ...	100	65	44	40	—

The growth is given in percentages of the optimal growth.

The smaller dose of calcium has the most marked effect. It shifts the optimum toward the acid side, and diminishes considerably the limiting action of high concentrations of hydrogen ions. The proportion of calcium in the 0·5 cc. per 50 gm. dose corresponds ly to 267 lb. per acre. The experiments of the writer tended to find the effect of H_2PO_4 and potassium or vity of hydrogen ions. Acid phosphate has somewhatfluence as calcium in neutralizing the effect of hydrogent no such influence was shown by potassium—a resurd with the findings of Prianischnikow. The potacaused a more vigorous growth of the plants, which d the ill-effect of the hydrogen ions.

This interaction of calcium ions in the physiological action of hydrogen ions is found also among fu In experiments with Gibberella (Lundegårdh, 1924, b g.,) the addition of calcium shifted the optimum p_H toward the acid side. The antagonism is still more remarkable here since calcium is not an essential nutrient for fungi. The behaviour Gibberella differs from that of wheat in that the phosphate ion has no antagonistic effect upon the hydrogen ion; ammonium, however, does exhibit an antagonistic action. Another point of interest is that the toxic action of aluminium ions increases in acid solution.

These experiments throw new light on the mutual inter-action of hydrogen ions and the ions of the nutritive salts in nature. The assumption of Olsen and others that the salt content of a soil is quite secondary in importance beside the p_H of the soil has no justification. The toxicity of the hydro-gen ions is reduced by the ions of various salts in the soil; and the nutrient action of the salts follows the law of relative effects. In the distribution of species, therefore, it must be borne in mind that the salts in the soil will always interact with the hydrogen ion concentration, and that there may be no comparison whatever between two soils of the same p_H.

From the practical standpoint this discovery of the inter-action of hydrogen ions and the ions of neutral salts is of great significance. Over-emphasis of one aspect of the effect of p_H has led to a distorted conception of the problem of liming. The neutralization of acid soils by large quantities of calcium is by no means the only way of eliminating hydrogen ions. Much smaller doses of calcium would be sufficient to anta-gonize the hydrogen ions, and very often manuring with acid phosphate will have the same effect, and will considerably improve an acid soil.

The experience of actual practice also argues in this direction. Christensen (1918; 1924), investigating the lime requirements of soils in Denmark, found that the effect of liming depended upon the concentration of other soluble nutrients in the soil. A rich soil, when it is distinctly acid, gives a much smaller response to lime than a poor soil; and in this respect the phosphate content of the soil seems to be of particular importance. Several American workers have found, too, that it is advantageous to manure acid soils with phosphates. It is possible that the phosphate ions may annul the toxic action of aluminium ions in acid soils. In this problem an important and fertile field of investigation awaits the physiologist.

Pearsall (1922) has put forward an interesting conception of the cause of antagonism between hydrogen ions and calcium ions. He considers that in acid soils it is not the hydrogen ions as such which are effective, but the low concentration of calcium. He examined the ratio of potassium to calcium and found that high values of this ratio had an injurious effect upon plants. According to Pearsall, plants on an acid soil are characterized by a high fat content. If potassium is in excess, the fats form easily diffusible soaps which facilitate

their translocation in the tissues. An excess of calcium, on the other hand, precipitates the soaps; in this way the impermeability of the cell surface is preserved. Pearsall's theory is reminiscent of the conception of Hansteen-Cranner, that the calcium is the "guardian" of the permeability of the cell.

Reference has still to be made to the fluctuations which occur in the p_H value of a habitat, and the changes brought about by the roots of plants. It is true that rain-water, when it reaches the soil, rapidly acquires the p_H of the soil; but in regions of heavy rainfall the actual concentration of hydrogen ions in the soil water may be somewhat less than that found by experiment. Conversely, in drought, the antagonistic action of other ions in the soil will alter the effective hydrogen ion concentration. It would be of great importance to know the relation between the hydrogen ion concentration and other physical factors in the soil, but there will have to be a great refinement in the present methods of analysis before this information can be acquired.

There appear, moreover, to be local differences determined by other causes. Olsen (1921) has observed that two samples from the same patch of soil can vary by as much as 0.2 to 0.3 units of p_H; though it is not certain whether these differences are real or depend upon the methods of analysis. It is significant that in artificial culture, differences of 0.1 unit of p_H, in the region of the optimum, cause marked differences in the growth. There is still considerable confusion upon this point.

It has frequently been observed that plants themselves change the p_H of the solution in which they are growing; this follows from the fact that the ions of the various salts are not all absorbed at the same rate. When the source of nitrogen is potassium nitrate, the reaction becomes alkaline, for [NO_3] ions are absorbed more rapidly than [K] ions. When ammonium chloride or ammonium sulphate is used, the solutions become more acid—a fact which has been observed in agricultural practice. The plant itself possesses a certain power of adjustment, for it can excrete [CO_3] ions into an alkaline solution, and Ca ions into an acid solution; this power of adjustment is naturally only very restricted (Hoagland, 1923).

It is not known with any certainty whether these changes in the p_H value observed in culture solutions occur also in the soil. Practical experience seems to indicate that the p_H value does change to some extent when the manure applied to the

soil breaks up into anions and cations which are unequally absorbed. The amount of displacement of the p_H value which a plant can cause in the soil will obviously depend upon the extent to which the soil is buffered. Weiss (1919) has shown that a well-buffered alkaline solution will not support the growth of maize and oats, since the plants are unable to change the p_H. In a weakly buffered solution the p_H was shifted by the plants themselves into the region of optimal growth.

The significance of hydrogen ions in ecology may be summarized as follows:

1. The actual hydrogen ion concentration of the medium is an important factor in growth. The relation between p_H and growth is that of an optimum curve, though the optimum is often very "flat." The position of the optimum and the limits of p_H within which a plant will grow are specific to the species.

2. The action of the hydrogen ions is influenced more or less strongly by the ions of neutral salts in the soil, so that the ecological effect of the hydrogen ions can only be assessed when consideration has been taken of the total salt content of the soil.

3. Hydrogen ions have a purely chemical effect upon the solubility of certain other substances in the soil, as, for instance, the compounds of aluminium and iron; and the effect of these latter substances upon the plant can easily be confused with that of the hydrogen ions themselves.

4. The potential hydrogen ion concentration of a soil, the buffering, is important for the maintenance of a constant reaction; so that the quantity and quality of the buffer materials, as reflected in the titration curve of the soil, are probably of importance for the welfare of higher plants and the micro-flora.

5. The hydrogen ion concentration of a soil can often be considered as an indicator of the phase of development of that soil—the degree of leaching out, and the type of humus decomposition, for the hydrogen ion concentration varies, together with the drainage and aeration, in accordance with the development of the soil.

4. The Chemical Analysis of Soils

It is a most difficult task to estimate that proportion of salts in the soil which plays a part in the life of the plant. The

older methods of chemical analysis are unanimously regarded as completely inadequate; these will be found fully described in Ramann's work (1911), Mitscherlich (1920) and Russell (1927). There is no comparison between the treatment of the soil with strong acids and the action of the roots of plants on the soil. Nor does treatment with 1–2 per cent citric acid achieve the desired effect. The difficulty of imitating the action of plant roots lies in this: that the absorption by plant roots is carried on slowly and without interruption, changing with changing external conditions and with the successive phases of development.

Mitscherlich has since abandoned the method of extraction he put forward in 1920. Carbonic acid is certainly the most active dissolving agent of the roots, but there are great difficulties in reproducing natural soil conditions experimentally.

Another method of obtaining the actual salt concentration of a soil is an analysis of the soil water mechanically removed from it; but this gives nothing more than a momentary glimpse of the condition in the soil (Gola, 1910; van Suchtelen, 1912; Ramann et al., 1916).

By the term "potential salt content" of a soil is understood the concentration of those loosely combined salts which break down into ions, according to the law of mass action, as soon as the actual ionic concentration sinks below a certain level. The salts are combined both chemically and by adsorption. In order to remove the ions adsorbed on the zeolites and the humus, various workers have suggested treating the soil with salt solutions (see Russell, 1927, for literature). These methods are useful for determining the "available" chalk in the soil. Still more difficult to estimate are the nitrogen compounds which arise from the activity of bacteria. Direct chemical analysis fails, for the actual nitrogen content of a vigorously "nitrifying soil" can be very small, if the soil is interwoven with absorbing roots. It is only by the combination of bacteriological and chemical tests that any idea can be gained of the nitrifying power of a soil. The problem has been discussed by Hesselmann (1917; 1926).

The lack of direct chemical methods has led some investigators to use the plant itself as a means of extracting salts from the soil. Neubauer (1923; 1925) planted seedlings in the various soil samples to be analysed, and after a certain time analysed the seedlings. In this way it was hoped to obtain

some idea of the manurial requirements of the soil.   It has since been proposed that bacteria be substituted in place of seedlings, as the "biological reagent"; to this question we shall return in Chapter VIII.   All methods which employ the living plant as a reagent have this defect: that the plant possesses great power of adjustment to different conditions, and different plants make very different demands upon the chemical compounds in the soil.   Plants are described in agriculture as possessing different powers of disintegration. Lupins and root plants, for instance, decompose the soil more than grasses, and among the grasses oats decompose the soil more than barley.   The most reliable form of experiment is the field trial, where, under measured external conditions, the response of the plant to given increments of salts can be observed.   A simplified method of procedure is that adopted by Mitscherlich (1924).   Mitscherlich cultivated plants in about 6 kilograms of the soil to be investigated, and took the yield as a criterion of the nutrient content of the soil.   Such a method obviously ignores other differences in the soil beside the chemical composition, but it is useful in that it gives a general index of the reaction of the plant to the chemical character of the soil.

In plant geography the problem of paramount importance is the distribution of the species, and the whole attention of the investigator is concentrated upon the factor in the environmental complex which is in minimum.   This makes the problem of the soil analyst easier, for the analysis of a water extraction of the soil will yield information of value to the ecologist.   The physical properties of the soil can be more or less determined from the p_H value, the aeration, the humus content, the clay content and the amount of nitrification; so that it is possible to obtain a schematic picture of the soil which is of the greatest value in the study of plant distribution.

In analysing a soil, consideration must be taken of the differences at different depths, for the roots of different plants penetrate for varying depths into the soil; deeper roots reach a richer substratum than those which are more superficial. Christ and Weaver (1924) have carried out experiments on the effect of nutrient accumulation at different levels.   They found that barley absorbed nutriment to a depth of 1 metre. Work such as this has a very great practical value, since it indicates at what depths in the soil manures should be laid.

CHAPTER VIII

SOIL MICRO-ORGANISMS [1]

THE fundamental importance of micro-organisms in the evolution of the soil, and in determining its ecological character, is very well known. Even the weathering of minerals is often facilitated by bacteria, though some controversy still persists over this problem. Phosphorus occurs generally in barely soluble forms such as apatite and iron phosphate. The strong acids produced by certain bacteria, nitric and sulphuric acids, attack these minerals, and hasten the purely chemical hydrolysis of them. In a compost of earth mixed with sulphur and insoluble phosphate, so much sulphur is oxidized by *Thiobacillus thiooxidans* and other bacteria, that the sulphuric acid formed converts a considerable part of the phosphate into the soluble form (Russell, 1923).

Even the carbon dioxide which is formed abundantly by bacteria assists the process of hydrolysis in mineral weathering (Ramann, 1911; Fred and Haas, 1919); in particular, the carbonates of potassium, magnesium, and iron, are brought into solution as bicarbonates, and so become accessible to roots, or can take part in further important processes in the soil. The carbon dioxide liberated by bacteria therefore supplements that respired by the roots.

The respiration of roots in a field of wheat amounts to no more than a third or a quarter of the total respiration of the soil (Lundegårdh, 1924, *a*, p. 201). Thus most of the soil carbon dioxide is derived from bacteria, and the "development" of the soil can take place in regions which have not yet been penetrated by the roots of higher plants; and the roots of seedlings, as they burrow their way into the soil in the spring, find free mineral material already prepared for them. For the absorption of mineral matter it is probably a significant fact that the

[1] This subject has been fully discussed by Russell (1927) and by Waksman (1927), to which books the reader is referred for a fuller bibliography.

immediate neighbourhood of the roots, the so-called "rhizo-sphere," is a region invariably colonized by bacteria.   Accord-ing to the investigations of the author (1924, *a*, p. 209), a con-siderable proportion of the respiration measured from the roots of plants is due to bacteria on the root surface; in wheat the value is as high as 45 per cent.   In a sterile soil the respiration of the growing roots is significantly weaker.

In the decomposition of a soil, it is probably of importance that the root hairs should form a continuous colloidal substrate with the mineral particles (Comber, 1922).   Bacteria, too, certainly occur in the closest contact with the mineral particles of the soil, producing at the surface of contact much higher concentrations of acid than occur at some distance.   Newton (1923) has shown that the roots of peas produce more carbon dioxide than those of rye, and this might explain the fact that the former dissolve out from the soil more calcium and magnesium.   (*See also* Parker, 1924.)

Humus is not a permanent constituent of the soil in the sense that quartz grains are.   Humus is a very complicated decomposition product of dead organic materials, mostly of plant origin.   Its composition does not remain constant; the process of breaking up goes on continuously, and the end products are simple inorganic materials.   So humus is continu-ously disappearing, only to be replaced by newly formed humus; and the balance between these two processes deter-mines the relative amount which is present in the soil.

Since the principal constituent of the plant body is cellulose, cellulose-destroying bacteria occupy a prominent place in the micro-population of the soil.   In regions where these bacteria are not present, on moors, for instance, thick layers of half-decomposed humus are formed, which close the formation to higher plant life.

Our knowledge of the bacteria which decompose cellulose is very incomplete.   The types discovered by Omelianski (1895; 1897) which decompose cellulose to form hydrogen or methane, are anaerobic, and would play only a minor part in a normal, well-aerated soil.   Hutchinson and Clayton (1919) described an aerobic cellulose bacteria, *Spirochaeta cytophaga*; and Macbeth and Scales (1919) have isolated fifteen aerobic cellulose-destroying organisms.   (*See also* Pringsheim, 1921; Löhnis, 1923; Dubos, 1928.)   There is evidence, too, that fungi take part in the disintegration of cellulose (Otto, 1916; Traaen, 1914; Neller, 1918; Waksman, 1925; 1926).

In no case, apparently, do the cellulose-destroying organisms effect a complete disintegration of the cellulose. Decomposition stops at the formation of certain intermediate materials, mostly acids, which are then used as respiratory material by other bacteria. This step-like decomposition of organic raw materials is very characteristic of all processes involving the action of micro-organisms. A humus is formed by the action of *Spirochaeta cytophaga* upon fresh straw, and this has been recommended as a substitute for farmyard manure (Hutchinson and Richards, 1921). Since the bacterium requires, in addition, nitrogen, a certain amount of ammonium nitrate is added. The rate of decomposition of cellulose is increased by the addition of ammonia, and the influence of farmyard manure upon cellulose decomposition in the soil depends upon its content of nitrogen as [NH_3] (Bartel, 1924; 1929).

The intensity of decomposition of cellulose far exceeds that of other bacterial decomposition in the soil. The ratio C/N for most living plants is about 40 (though it is as low as 25 in the leguminosae); in the soil this ratio is gradually reduced to about 10. The excess of carbon escapes into the air as carbon dioxide, where it is again used for plant nutrition.

The composition of humus is not yet fully known, though a number of its components have already been isolated. The idea once common, that humus consists chiefly of carbohydrates, is not now supported (Marcussen, 1921). Modern bacteriologists incline to the view that organic nitrogen products enter into its composition.

According to Waksman (1928), forest humus consists of:

(1) a number of plant remains, such as cellulose, hemicellulose, fats, wax, susceptible to decay; and

(2) more resistant substances, such as lignin, cutin, tannin, and resin;

(3) fungal mycelium, spores, cells of bacteria, protozoa and worms; and

(4) decomposition products of organic remains, acids and ammonia.

1. The Nitrogen Supply in the Soil

The quality of a soil depends to a great extent upon the course followed in the conversion of nitrogen. For their supplies of this element the higher plants are completely dependent upon the activity of bacteria, for neither protein

materials nor the nitrogen of the air can serve as a source of nitrogen. The proteins of dead organisms are first of all broken down into amino-acids, and from these ammonia and carbonic acid are split off (Robinson and Tartar, 1917).

$$H - \underset{\underset{NH_2}{|}}{\overset{\overset{H}{|}}{C}} - \underset{OH}{\overset{O}{\overset{\diagdown}{C}}} + 3O = 2CO_2 + H_2O + NH_3 + 152 \text{ cal.}$$
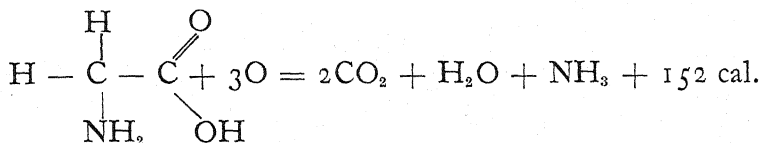
Ammonia arises as a by-product in the decomposition of amino-acids. Now the ammonifying bacteria are just as well able to break down carbohydrates, such as sugar, for their supplies of energy, and for this reason the intensity of
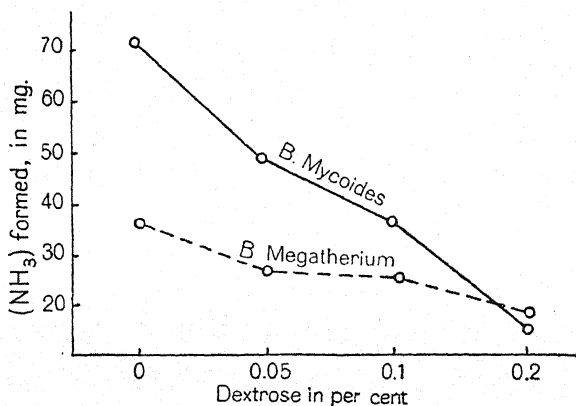
FIG. 71.—The production of Ammonia in pure bacterial cultures from 5 gm. Caesin, with varying quantities of Dextrose. (Doryland, 1916.)

ammonification falls in the presence of sugar (Doryland, 1916) (Fig. 71). The same effect is produced in the soil by undecomposed organic materials, rich in carbohydrates, such as straw. Waksman (1927; pp. 266, 376, 493) mentions that fungi and *Bactinomyces* may also take part in the formation of ammonia. In the soil the ammonia formed by these methods is soon combined as ammonium carbonate; and this is the raw material for the manufacture of saltpetre in the soil.

Nitrification in the soil takes place in two steps. The nitrite bacteria (*Nitrosomonas*), by partial oxidation of ammonia, form nitrous acid, which combines with bases, such as lime, present in the soil; then the nitrites, by the agency of the nitrate bacteria (*Nitrobacter*), are further oxidized into nitrates.

The two stages of nitrification so interlock, that only traces of free nitrite are to be found in the ground. The velocity of the whole process depends upon the intensity of ammonification, for this is the slowest of the three constituent processes (Russell and Appleyard, 1917; Gainey, 1917). Free ammonia occurs in the soil in traces of one or two parts per million.

Not only ammonification, but nitrification also, seems to be inhibited by the presence of carbohydrates, though it has been shown that this inhibitory effect takes place chiefly in culture solutions, under conditions which at best give a somewhat distorted picture of nitrification under natural conditions (Coleman, 1908; Stevens and Withers, 1910). In sewage water filters, and in soils rich in organic matter, vigorous nitrification can occur.

It was formerly believed that pronounced nitrification took place only in cultivated soils; but the researches of Weiss (1908; 1910; 1917; 1924), Hesselmann (1917; 1919; 1926; 1927), Gaarder and Hagem (1921; 1928) and others have shown that nitrates are also produced on a large scale in forest soils.

According to these authorities a real deciduous forest soil produces nitric acid as fast as the soil of a well-cultivated field. The highest values were obtained in a mixed wood of oak, hornbeam, elm and beech; in alder woods, too, high intensities of nitrification were measured. In the hygrophilous meadows described by Hesselmann, where the vegetation is very rich, a considerable amount of nitrification takes place in the soil. In birchwoods Gaarder and Hagem have found a certain amount of nitrification, though here there is some accumulation of the nitrite stage of the process.

Hesselmann divides the soils of coniferous forests into two types. Soils of the first type contain lime, and carry a thick ground vegetation. They are true moulds, though nitrification seems to be much weaker than in soils of deciduous woods; moreover, the nitrophilous species in these soils rarely exhibit nitrate reactions when the tissues are treated with diphenyl-amine-sulphuric acid.

Soils of the second type are carpeted with moss, and in these soils nitrification does not take place at all. Gaarder and Hagem (1921) have put forward the supposition that in the formation of an acid humus, insufficient nitrogen compounds of the [NH_3] group are formed for nitrification to proceed.

It is remarkable, however, that there should be a total absence of nitrification when solutions containing ammonium compounds are inoculated into such a soil.

It appears improbable, too, that the high hydrogen ion concentration of these soils eliminates the ammonifying and nitrifying bacteria, since active nitrification can be carried on in very acid cultures. Generally speaking, there exists no close relationship between nitrification and the p_H, or the buffer capacity, of a soil (Gaarder and Hagem, 1921; Weiss, 1924). Gaarder and Hagem have noted, however, that in the majority of their tests, where active nitrification existed, the p_H lay between 6·8 and 6·4. They have suggested that there are several races of nitrogen bacteria, with different optimal p_H values.

Another factor contributing to the absence of nitrification in acid humus soils is the low salt content. The calcium or magnesium salts necessary for the neutralization of the nitrites are not present, and the potassium salts and phosphates necessary for all bacteria are present only in small quantities. When humus is mixed with a soil rich in minerals, an active nitrification begins (Hesselmann, 1917).

The ammonifying and nitrifying bacteria will tolerate high concentrations of carbon dioxide; in fact they are only noticeably harmed by concentrations as high as 30 per cent (Plummer, 1916; 1917). They are, however, sensitive to oxygen deficiency, so that nitrification is promoted by a good aeration of the soil. Toulaikoff (1915) has observed that the intensity of nitrification increases greatly after the ploughing of a field. In damp soils the oxygen content of the ground water seems to be of great significance; even on peaty soils and on moors, active nitrification can be observed when the ground water is moving freely and is charged with oxygen (Hesselmann, 1917). In mountains, too, the most active formation of nitrates is to be found in those regions where the soil is always damp from streams or from snow.

According to Hesselmann, the different types of vegetation in Sweden have each their specific intensities of nitrification; and the same investigator has observed that mycorhiza occur more commonly in soils which are poor nitrifiers, than in soils in which the nitrification is good. More recent work (Hesselmann, 1927; Melin, 1927) has shown that a high nitrogen content will stimulate the development of mycorhiza.

Let us turn now to the question of mycorhiza. Ectotro-

phic mycorhiza are widely distributed upon the roots of forest
trees; and yet the question has not yet been settled as to whether
the fungus of this mycorhiza is capable of independent nitrogen
fixation. In pure culture no fungus except *Phoma betae* has
been shown to fix free nitrogen. This, however, does not
even constitute good negative evidence. Benecke has made
a similar objection (1924, p. 408) that the bacterial nodules on
the *Leguminosae* will not fix nitrogen in pure culture, though
nitrogen is undoubtedly fixed under natural conditions.
There are a great many instances in which the behaviour of
the bacteria in culture is quite different from their behaviour
in the soil.

Even if the mycorhizal fungus does not really fix
nitrogen from the air, it may be supposed that it "works up"
the nitrogen compounds in humus in a way differing from that
of the ammonifying and nitrifying bacteria. It is well known
that fungi form ammonia (Russell, 1923, p. 137), but there is
the greatest uncertainty as to further stages in the process.
Melin (1921; 1922; 1923; 1925) has found that the
mycorhizal fungus of firs will thrive in culture upon organic
nitrogen compounds; so there is some possibility that a fungus
growing where nitrification is poor will accept organic material
as a substitute. There is now no doubt that there exists be-
tween the ectotrophic mycorhiza and the host plant a narrow
symbiotic relationship.

Mention might be made here of the theory of Stahl (1900)
that the fungus collects salts for the host plant. The myce-
lium forms a weft over the whole forest soil, and, in the
light of our knowledge of the power of decomposition which
fungi have, the postulate of Stahl does not seem improbable.

The carbon cycle in nature lies half in the atmosphere, and
the carbon dioxide of the atmosphere is a gigantic reservoir,
of immense importance in the carbon balance in nature. The
nitrogen cycle, on the other hand, lies to a great degree,
though not exclusively, in the soil.

Attention will now be directed to the fixation of atmos-
pheric nitrogen.

Of the nitrogen-fixing bacteria described up to the pre-
sent, *Clostridium pasteurianum*, discovered by Winogradsky, is
anaerobic, and *Azotobacter* and *Granulobacter*, described by
Beijerinck, are aerobic.[1] Both aerobic forms have a world-

[1] For references to this question, see Benecke-Jost, Russell (1923), Dügelli,
and Omelianski (1919).

wide distribution, except that *Azotobacter* does not occur in acid soils.

Investigations by Lipman and Waynick (1916) show that there is a parellelism between nitrogen fixation in the soil and the occurrence of *Azotobacter*. There is no doubt whatever of the importance of this bacterium in the nitrogen economy of both natural and cultivated soils; though, as Russell has pointed out (1927, p. 200), its presence in a soil does not mean that it is active in fixing nitrogen. It has already been mentioned that *Azotobacter* is very sensitive toward the hydrogen ion concentration; in acid soils its activity is suspended. Nor has *Azotobacter* much resistance against poor aeration of the soil. It has been observed by Ashby (1907) that nitrogen-fixing activity decreases rapidly with increasing depth below the surface of the soil.

The symbiosis of the anaerobic *Clostridium* with the aerobic *Azotobacter*, which appears to extend the activity of the former, is a phenomenon of very great interest; the rate of nitrogen fixation is said to be increased also by the association together of *Azotobacter* and *Granulobacter*, of *Azotobacter* and forms of *Nostoc*, or even of two forms of the same species. (For literature, *see* Russell, 1923.)

Azotobacter is very specialized in its demands upon the environment. Beside demanding an adequate calcium content in the soil, and a rich supply of organic material, it requires a high temperature. Below 7° C. nitrogen fixation in the soil ceases. A large amount of energy is required in nitrogen fixation, and correspondingly large amounts of carbon dioxide are liberated (Hutchinson, 1918; 1919).

With *Azotobacter* the difficulty is again encountered as to how far the conditions in culture can be used to interpret the behaviour of the bacterium in nature. It does seem to be certain that nitrogen fixation by *Azotobacter* and similar organisms only takes place really actively in the better mould soils. According to Christensen the bacterium requires a certain amount of phosphate, though the presence of nitrates inhibits the fixation of atmospheric nitrogen. This inhibition is due to the fact that *Azotobacter* obtains its nitrogen by splitting up nitrate, when nitrate is present in the soil (Bonazzi, 1921). However, even in soils in which rapid nitrification occurs, there is very little free nitrate in the soil, so that in nature this obstacle to nitrogen fixation can be neglected.

In soils too poor to support the growth of *Azotobacter* and allied organisms, fungi and algæ may play some part in the fixation of nitrogen. Nitrogen deficiency in such soils exerts a strong limiting effect upon growth. The algæ themselves do not fix nitrogen; but in some form of symbiosis with nitrogen bacteria, large quantities of nitrogen are fixed (Kossowitsch, 1894; Bristol and Page, 1923). The discovery by Hellriegel and Wilfarth of the symbiosis between the *Leguminosae* and the nitrogen-fixing bacterium *Bacillus radicicola*, is of great importance ecologically. By virtue of their symbiosis, the *Leguminosae* are enabled to flourish in a soil very poor in humus, provided sufficient potassium, phosphate and lime is present. The beneficial action of leguminous plants was known to plant culture in ancient times, but the part it plays in the type and succession of plant societies is not known, even to this day. It might reasonably be conjectured that leguminous plants prepare the soil for an independent nitrogen fixation.

The nitrogen combined in the living bodies of the nitrogen-fixing bacteria in the soil is naturally of no immediate use to the plant; and only after the death and decomposition of the bacteria, is the nitrogen contained in them made available.

If the fixation of nitrogen from the atmosphere were not compensated by other processes, which tended to decrease the capital of nitrogen in the soil and in the plant body, an excess accumulation of nitrogen would very soon occur. Hall reports (1905) that a field at Rothamsted, cropped continuously, gained in twenty-two to twenty-four years about 2,000 lb. nitrogen per acre, i.e. about 90 lb. per year.

There exist, however, denitrifying bacteria, which are capable of reversing the process of nitrification; these liberate gaseous nitrogen from the soil, which escapes into the atmosphere. This evolution of nitrogen acts as a sort of safety valve, for it occurs chiefly in soils very rich in nitrogen. Nitrogen is also evolved from manure heaps and sewers. The loss of nitrogen from manure is a serious matter in agriculture, and it is a problem of great practical importance to store manure in such a way that the loss of nitrogen is reduced to a minimum. Our present knowledge of the problem is, however, altogether inadequate, although it can generally be said that anaerobic conditions will favour denitrification, while a good supply of oxygen causes nitrification (*see also* Russell, 1927, p. 260; Waksman, 1927).

Beside these more fundamental steps in the nitrogen cycle, there occur a number of other processes in the soil, whereby nitrogen compounds of high nutritive value are converted to compounds of lower nutritive value. The most widespread of these processes is the formation of nitrites and ammonia from nitrates. This consumption of nitrate, in which both bacteria and fungi share, seems generally to occur when the soil is poorly aerated. Beside nitrites and ammonia, nitrogen and nitrous oxides are formed. Even if the ammonia escapes into the air it may be put to use again, for the rain dissolves it and brings it back into the soil (Nienburg, 1919). According to Mayer, an average of 1·8 lb. of nitrogen per acre are deposited per year in the form of ammonia (cited by Benecke-Jost, 1924, I, p. 236). Nitric acid, derived from electro-chemical processes in the upper layers of the atmosphere, is also brought down by the rain into the soil. (Boussingault, 1861; Muntz and Marcano, 1889, found 16 mg. per litre HNO_3 in the tropics.)

To what extent denitrification of nitrates takes place in normal soils is not adequately known. Russell inclines to the view that the decomposition of nitrates does not occur to any pronounced degree in well-drained cultivated soils, but that it may occur in water-logged soils. According to Doryland (1916), ammonifying bacteria, in the presence of carbohydrates, will assimilate ammonia and nitrates.

All humid soils suffer considerable loss of nitrates during the winter, owing to leaching out; and at this time the streams become charged with nitrates, not usually found in water. An experiment undertaken at Rothamsted gives an idea of the amount of nitrate which is washed out of an uncropped soil. A mass of soil, about 4 cubic metres in area, was built into a lysimeter, so that the amount of rain-water permeating through it could be collected. In the course of 47 years the soil has lost annually between 35 and 45 lb. of nitrate per acre, by leaching out; and soils richer in nitrates probably lose still more (Russell and Richards, 1920).

When the soil is covered with vegetation, the nitrates are reabsorbed by the roots as soon as they are formed, and so the leaching out is much less obvious. In autumn and spring, when the soil lies uncovered by vegetation, large quantities of nutritive materials are washed out, and it is one of the aims of modern agriculture to reduce this loss to a minimum. A good "salt buffering" of the soil, especially a high adsorptive power,

contributes toward this reduction. The contents of micro-organisms, bacteria, fungi, and algæ, which absorb nitrogen, and yield it to the soil as ammonia when they die, are probably not without significance; though there is danger that these organisms contend with the higher plants for nitrogen during the growing period.

Beside the processes described above, whereby the higher plants in a well-aerated soil are ensured of their nitrogen supply, there are other processes in the soil of ecological importance, depending upon the presence of micro-organisms. In water-logged soils and beside bogs and lakes, aerobic bacteria and fungi, and the decomposition processes due to them, disappear. In consequence of this, development takes another course. Instead of a complete decomposition of the organic remains, a rotting sets in, giving rise to fœtid substances such as indol and skatol as intermediate products. The sulphur-containing proteins yield hydrogen sulphide, the phosphorus-containing proteins, phosgene, and the carbo-hydrates, methane and hydrogen. In short, instead of the complete mineralization of a well-aerated soil, there arise as a result of oxygen deficiency, a series of reduction products which are more or less powerful plant poisons.

In stagnant water and in water-logged beds of seaweed at the edge of the sea the sulphuretted hydrogen given off increases the hydrogen ion concentration, and acts moreover as a poison, so that a number of the more sensitive hygrophytes are excluded. The "bog toxins" postulated by American workers may likewise represent acid reduction products. Schreiner and his collaborators have isolated dy-hydroxy-stearic acid from poorly aerated soils (1907; 1910; 1911). This is very toxic for mesophytes and hygrophytes; a concentration as low as five parts in one hundred thousand definitely inhibits the development of wheat. On the addition of oxygen the substances are destroyed.

The poisonous quality of peaty waters for most plants depends upon the presence of reduction products (Dachnowski, 1908; 1909). An interesting demonstration is given by Montfort (1921; 1922), that peaty water inhibits the water uptake of non-moor plants, while with true moor plants the uptake of water remains unchanged; thus refuting Schimper's idea of the "physiological drought" of moorland soils. (Reference should also be made to Stocker, 1924.) Generally speaking, moor plants are not xerophytes in the ordinary sense

of the word, but are probably, like all evergreen plants, adapted to the unfavourable water balance of the winter to which all northern sclerophyllous plants are exposed.

The toxins in moor water apparently disappear if the soil is well aerated. Dachnowski has suggested that the poisonous action of the water is due to the presence of certain anaerobic bacteria (1912). The toxic phenomena in water-logged and badly aerated soils, due to reducing bacteria, are probably coupled with self-poisoning of the roots, since, in a deficiency of oxygen, various intermediate products of respiration are formed such as acetic acid, acetaldehyde, acetone, and so on (Stoklasa and Ernest, 1908; Czapek, 1920; van der Wolk, 1920). Even in sterile water cultures this self-poisoning can occur. The roots of bog and moor plants, on the other hand, are completely adapted to an anaerobic existence.

The appearance of poisonous reduction products is the last stage in the bad aeration of a soil. A decrease in the aeration results first of all in an excess of carbon dioxide, and then deficiency of oxygen. The most sensitive plants are eliminated even by the accumulation of carbon dioxide; it is often difficult to decide whether a plant is suffering from poisoning due to the bog products, or merely from poisoning due to excess of carbon dioxide.

When oxygen is lacking, the soil is not only impoverished of nitrates, but also of sulphates, which are reduced to sulphuretted hydrogen by the organism *Microspira desulphuricans*. This reduction takes place abundantly in the sludge of both fresh and salt water. In the light, the ascending sulphuretted hydrogen is oxidized back again to sulphates, or intermediately to sulphur, through the agency of sulphur bacteria (Samjalow, 1913).

It is generally accepted that the poisonous reduction products of soils poor in oxygen may be re-oxidized and rendered innocuous after they have come into contact with fresh, aerated soil. There seems to be no organic material which cannot be destroyed through the agency of soil bacteria. Compounds as stable as paraffin, phenol, naphthalin, and toluol are oxidized without difficulty. The deposition of such organic substances as amber, petroleum, and coal is only possible in soils suffering from a perpetual deficiency of oxygen. This universal ability of fresh soil to decompose organic material is one of the essential conditions for the maintenance of life upon the Earth.

2. THE MICRO-POPULATION OF THE SOIL AND ITS ENVIRONMENT

Micro-organisms, like higher plants, are subject to the environment in which they grow, and the stimulating action of nutrient salts is a most important constituent of this environment (Lundegårdh, 1924, *a*, p. 191). Phosphates and salts of potassium are, as a rule, favourable to the growth of bacteria (Fred and Hart, 1916; Koch, 1917; Dumont, 1897). Alkali salts favour the development of actinomycetes. Nitrates increase the intensity of ammonification (Coleman, 1917), the activity of *Azotobacter* (Greaves, etc., 1922; Hills, 1916), and that of the nitrate-reducing organisms (Greaves, etc., 1919). The presence of inorganic salts promotes the breakdown of cellulose (*see* p. 237). Calcium generally exerts a favourable effect upon bacterial growth, partly on account of its regulatory action upon the hydrogen ion concentration. Even ions of aluminium can promote the growth of bacteria; according to Denison (1922), they stimulate ammonification, though they inhibit nitrification.

Some of the ions which are favourable to bacterial growth may be regarded as nutritive materials, while others can be labelled as "stimulants." A great deal of work is needed to distinguish between the two types of action. In the bacteria, as in higher plants, an important part is played by the ions in producing and preserving a suitable condition of permeability. Moreover, the phenomenon of antagonism between the ions has been shown to play a part in the life of bacteria. In ammonification and in nitrification Greaves (1920) found an antagonism between calcium and iron, between calcium and magnesium, and between calcium and sodium. Antagonism is more pronounced between a monovalent and a bivalent ion than between two bivalent ions. The principles of colloid chemistry, described on page 196, are valid for bacteria as they are for higher plants and for fungi.

The study of the action of ions upon the activity of bacteria is so recent, that it is impossible to say whether the influence of ions follows some general law which will hold throughout the whole range of living matter. The probability is, however, that certain ions, such as calcium, phosphate, potassium and hydrogen, exert a definite action upon the state of the plasma. If this is so, a fundamental significance will attach to these ions, quite apart from their purely nutritive value.

Omitting for the moment the purely physiological side of the problem, and regarding it from an ecological standpoint, it may definitely be stated that, in general, both higher plants and bacteria behave in a similar manner toward the ions present in the soil. A soil rich in ions, therefore, does not only promote the growth of higher plants in the habitat, but accelerates also the activity of the bacteria, and thereby the disintegration of humus.

Wollny (1886) and Ramann (1889), by measuring the carbon dioxide produced in the destruction of humus, have demonstrated that the addition of salts accelerates the process. Wollny added potassium salts to the soil and obtained a higher production of carbon dioxide; Ramann found an increased decomposition of organic residues on the addition of manurial salts.

The effect of application of salts upon the carbon dioxide output in the soil was closely investigated by van Suchtelen (1910). He added varying quantities of superphosphate, ammonium sulphate, and magnesium sulphate, to every six kilograms of soil, and obtained a significant increase in the amount of carbon dioxide evolved. Researches of the same type, carried out by the writer (1922, *b*; 1924, *a*, p. 193) have shown that quantities as small as three milligrams of salt to 100 grams of soil will increase the carbon dioxide output of the soil by 20–120 per cent. This result is of importance, since it shows that small variations in the natural salt content of the soil will influence the decomposition of the humus to a considerable extent. Since all bacteria, especially those of ecological importance, such as *Azotobacter* and the nitrate bacteria, respire large quantities of carbon dioxide (Stoklasa, 1908), measurement of the carbon dioxide production of the soil gives a good general idea of the amount of bacterial activity (Waksman and Starkey, 1924; Waksman, 1927, p. 717; Melin, 1928).

The soil bacteria constitute a very harmonious working colony. They work together as a "team," in that each type of bacterium only plays a specific part in the complete chain of chemical synthesis or decomposition. The ammonifying, nitrite, and nitrate bacteria provide an excellent example of such "team work." Any change in the chemical composition of the soil which stimulates the ammonifying bacteria, at the same time indirectly increases the nitrification; and it is probable that many other similar co-operative processes occur

among the micro-organisms of the soil. It may be concluded, then, that within certain limits, the application of neutral salts increases the rate of decomposition of the soil.

The establishment of the fact that the whole bacterial flora of the soil responds uniformly, up to a certain point, to the application of salts, by no means presupposes that divergences do not occur. Indeed, an example has already been given where the addition of an ion promoted the growth of some bacteria, while it checked that of others. The "salt curves" and "hydrogen ion curves" of growth of the higher plants corres-pond as to their general form, and differ from one another as to the position of the cardinal point. In the same way the various species of bacteria are "attuned" differently to the action of various ions; and it is for this reason that the decom-position of humus takes place along such divergent lines, corresponding to differences in the soil, of salt supply, aeration, water content, and so on. It may often happen, too, that a change in the ion content of the soil will result in the increase of other micro-organisms, such as fungi.

The effect of a single salt upon bacterial activity is repre-sented by an optimum curve, just as it is in higher plants. In higher concentrations all salts are inhibitory to bacterial activity, a fact which has been established by Greaves and his co-workers (1916; 1920; 1922). The colloidal action of the ions plays some part in this toxic effect. The inhibitory action of the cations upon nitrification and ammonification decreases in the following order:

$$Mn > Mg > Fe > Ca > Na > K.$$
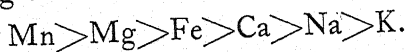
In addition to this, specific differences exist in the inhibitory action of the various ions. According to Greaves magnesium chloride checks nitrification before it does ammonification. Such differences are naturally of importance in arid soils, in which the salt concentration is high, for they determine the course which decomposition will take.

Bacterial activity is promoted not only by inorganic salts, but also by organic materials, which play a part as nutrients and as stimulating substances. It is of significance in ecology that substances excreted from the roots of plants are able to influence bacterial life; under some conditions the excretions may be inhibitory to growth (Löhnis, 1910), under other conditions they stimulate bacterial activity.

According to Wilson (1920), roots excrete materials

which stimulate the growth of *Bacterium fluorescens*, *Azoto-bacter*, and that of denitrifying bacteria. Neller (1922) also found that bacterial activity in the soil is markedly stimulated by the presence of roots. Finally, Melin (1924) reports that mycorhizal fungi (*Boletus variegatus*) and soil fungi (*Rhizoctonia silvestris*, *Mucor Ramannianus*) are greatly stimulated in their growth by organic materials which diffuse out from the seeds and seedlings of pine and fir. The stimulating materials may perhaps be identified with the water soluble phosphatides discovered by Hansteen-Cranner (1925; 1926).

The pectic substances arising from the root epidermis, and dead cells from the root cap, are undoubtedly excellent nutritive substances for bacteria. *Actinomyces*, for instance, thrives upon dead grass roots (Beijerinck, 1900; Conn, 1922).

The influence of dissolved substances on bacterial activity depends to some extent upon the moisture content of the soil. Since the bacteria are very small, and accumulate on the surface of the soil particles, they will only suffer from water deficiency if the water content of the soil is considerably lowered. The close relationship between bacterial activity and change of water content of the soil may depend to a great extent upon concomitant changes in the concentration of the salts dissolved in the soil solution. In a dry soil the concentration will eventually become supra-optimal; in a soil saturated with water, the bacteria will suffer from lack of oxygen.

The influence of temperature upon bacteria is more difficult to understand. It has been shown that *Azotobacter* is not active below a temperature of 7° C. Nitrification does not take place below 5° C., and above this level it has been shown to increase with the temperature (Russell and Appleyard, 1915; 1917; Panganiban, 1925). On the other hand, it was not possible to demonstrate a parallel increase in the number of bacteria with increasing temperature (Russell, 1927, p. 276; Cutler, Crump and Sandon, 1923). Fabritius and Feilitzen (1905), however, found a definite correlation between bacterial number and temperature in the soils of moors; and there is no doubt whatever that the rate of decomposition in the soil increases with temperature, a phenomenon which explains the poverty of humus in damp, tropical soils.

Freezing a soil affects it in a singular way; after the subsequent thawing out of the soil, the bacterial activity, instead of being reduced, is greatly increased (Conn). Temporary

drying out of the soil results in a similar increase (Prescott, 1920; Lebediantzev, 1924).

Hutchinson and Russell have suggested an explanation for these peculiar phenomena (Russell, 1921, p. 280; 1923, p. 66). These authors set out with the observation that partial sterilization of the soil, by heat or by chemical agents, produces first a check, and then a marked increase in the number of bacteria and the amount of ammonification. In pursuit of this fact they advance the theory that, beside the bacterial population of the soil, there is a population of protozoa which interferes with the activity of the bacteria. When the
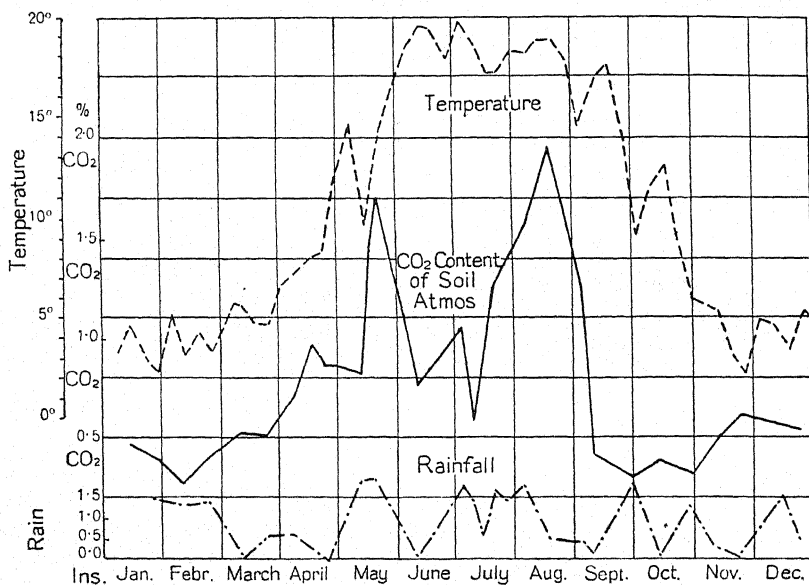
FIG. 72.—Carbon dioxide content of the soil atmosphere at a depth of 15 cm. in the course of the year (Russell and Appleyard).

protozoa are killed by heat or by poisons, the bacteria can develop without hindrance. More recent work (Russell, 1927; Waksman, 1926; 1927) has shown that the theory is unlikely to account for the phenomenon, especially in view of the relatively few protozoa in the soil.

According to Russell, the great increase in the number of protozoa in the soil after fertilization with quantities of farm-yard manure will explain the "soil sickness" frequently observed in greenhouses. After partial sterilization with carbon disulphide or by heat, the soil recovers and shows a higher productivity.

It has been known for some time that the activity of the soil exhibits two well-defined maxima, one in spring, and the other in late autumn (Figs. 72 and 73).

| April | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. | Jan. | Febr. | Mar. | April |
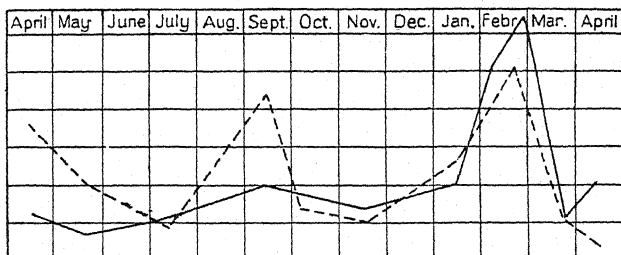
FIG. 73.—Bacterial Numbers in two Soils.

The spring maximum in the soil is obviously of significance for the higher plants, which at that time can benefit from the additional quantities of nitrates in the soil. Much of the nitrate formed in the late autumn, however, will be lost through leaching out, and may become available for hydrophytic plants and other aquatic organisms. The time of greatest leaching corresponds to the spring maximum of development of water plants.

Finally it may be mentioned that fungi, too, exhibit an annual periodicity similar to that of bacteria. Owing to the difficulty of measuring the *amount* of a fungus quantitatively, the magnitude of the periodic increases is not known. The reaction of fungi to salts in the soil differs from that of bacteria; in some soils, therefore, fungi dominate, while in other soils the balance is in favour of bacteria. Waksman has found (1922) that farmyard manure and acid manures increase the number of fungi in the soil, while lime tends to decrease the number.

3. INVERTEBRATE FAUNA OF THE SOIL

Darwin (1881) stressed the importance of earthworms for the mechanical mixing of the soil. Earthworms swallow the remains of plants, or draw the remains into their holes and mix them with humus and mineral particles of the soil. Darwin has calculated that the earthworms of an ordinary soil draw through their alimentary canals about 25 tons earth per hectare per year. Insects, too, and other arthropods living in the soil, contribute toward its pulverization; but, as far as chemical decomposition is concerned, these organisms play a very subordinate part.

The size of the soil fauna depends very much upon the environmental conditions. In good forest soils, and in manured and cultivated fields, it is particularly high. An idea of the populations is given in Table XLIV.

TABLE XLIV

THE NUMBER OF SOIL FAUNA PER HECTARE CULTIVATED FIELD AT ROTHAMSTED

	Unmanured.	Manured.
Insects	6,200,000	19,300,000
Large nemathodes	1,990,000	9,000,000
Myriapods	2,100,000	4,480,000
Oligochaete	1,145,000	2,513,000
Arachnidae	590,000	1,380,000
Crustaceae	84,000	202,000
Molluscae	33,000	84,000
Total	12,232,800	36,959,000

(From Morris, 1922.)

In conclusion, the ecological significance of soil micro-organisms can be summarized in a few pages. The chief function of micro-organisms is the destruction of dead plant and animal bodies. In a sterile soil undecomposed plant residues would accumulate to such an extent that no seedling could penetrate the layer. How injurious even a thin layer of half-decomposed organic matter can be, is to be seen in pine and spruce woods, where raw humus is formed. The litter of leaves forms a tough layer permeated by fungal hyphae, which excludes very many plants.

In beech woods, too, where raw humus is formed, ground vegetation is altogether lacking over wide stretches of the forest; for the seeds lying in the stratum of leaves which overlies the true soil cannot develop into hardy seedlings (Plate VIII b). This stratum of undecomposed leaves dries out completely in periods of drought; it is very impermeable mechanically, and it contains very few free nutritive materials. When the layer has decayed, the salts are liberated, the structure becomes spongy, and the water capacity rises.

It is this destruction of organic remains which renders possible a cycle of those elements which build up the plant body, and which is essential for continued life on our planet. The two fundamental substances taken from the atmosphere—carbon and nitrogen—are present in none too ample quantities. This applies especially to carbon, which is present in a

PLATE VIII
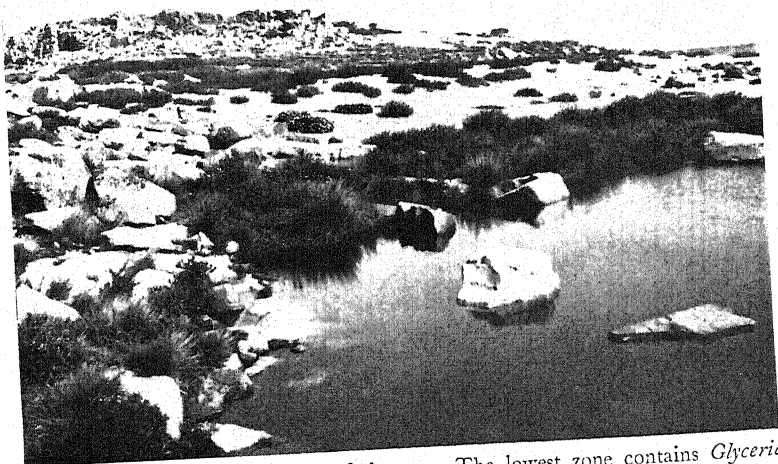
(a) Zonation in a calm creek of the sea. The lowest zone contains *Glyceria maritima* and *Triglochin maritimum*, and above, *Marticaria maritima* and *Salsola kali*. This is followed by a zone of *Armeria elongata*, and a gradual transition into an epilitoral zone of herbs (*Festuca rubra, Agrostis, Avena elatior, Hieracium umbellatum*, etc.), and bushes (*Rosa, Prunus spinosa, Cotoneaster*, etc.).

(b) Beech wood, without ground vegetation. The raw humus soil is covered by a thick layer of dead leaves.

relatively high percentage in living organisms, and yet occurs in very small concentrations in the air.

It has been calculated that the total consumption of carbon dioxide in the plant world reaches 58·9 billion kilograms per year; that is, about $\frac{1}{35}$ of the total amount of carbon dioxide in the atmosphere (Schroeder, 1919). If decay should cease, life would in a very short time become extinct. The activity of the cellulose-destroying organisms in the soil is one of the most important biological processes upon the earth, and if it were inhibited, life itself would be in danger. In the carboniferous period the creation of organic material was in excess of the decay, and the world's supply of coal corresponds to an amount of carbon dioxide four times as big as the total content of our atmosphere to-day (Lundegårdh, 1924, *a*, p. 44). To-day, perhaps, on our moors, a gradual accumulation of carbon is again taking place, at the expense of free carbon dioxide in the atmosphere.

As far as the total carbon cycle is concerned, it does not matter how the breakdown of the organic remains occurs. For plant geography, however, the course of decomposition is extraordinarily important. In Figure 74 have been distinguished three principal types of decomposition:

1. The formation of *real mould*, a process which occurs in well-aerated and reasonably moist soils, provided with sufficient salts, especially calcium. The humus materials formed by this method are neutral, imbibe water readily, and are insoluble in water. This soil supports a eutrophic vegetation.

2. The formation of raw humus and peat, which usually occurs when the aeration is sufficient, but when there is a deficiency of salts, so that the intensity of bacterial activity is reduced. On such a soil there arises an oligotrophic vegetation, which, moreover, must be adapted to the peculiar mechanical and physical conditions of the humus.

This method is distinguished chemically by the formation of humus acids. In a raw humus soil, the decomposition is incomplete, and certain intermediate products accumulate, which appear to be omitted altogether in real mould soils. An exact elucidation of this important point has yet to be put forward.

3. The formation of swamp and sludge soils, owing to oxygen deficiency and excess of water. The course of decomposition is anaerobic, and results in the formation of noxious

reduction products. In such habitats swamp and sea-shore vegetation develop.

From the chemical standpoint this course of decay is characterized by the incompleteness of humification. Reduction products, such as methane, fatty acids of various kinds, and
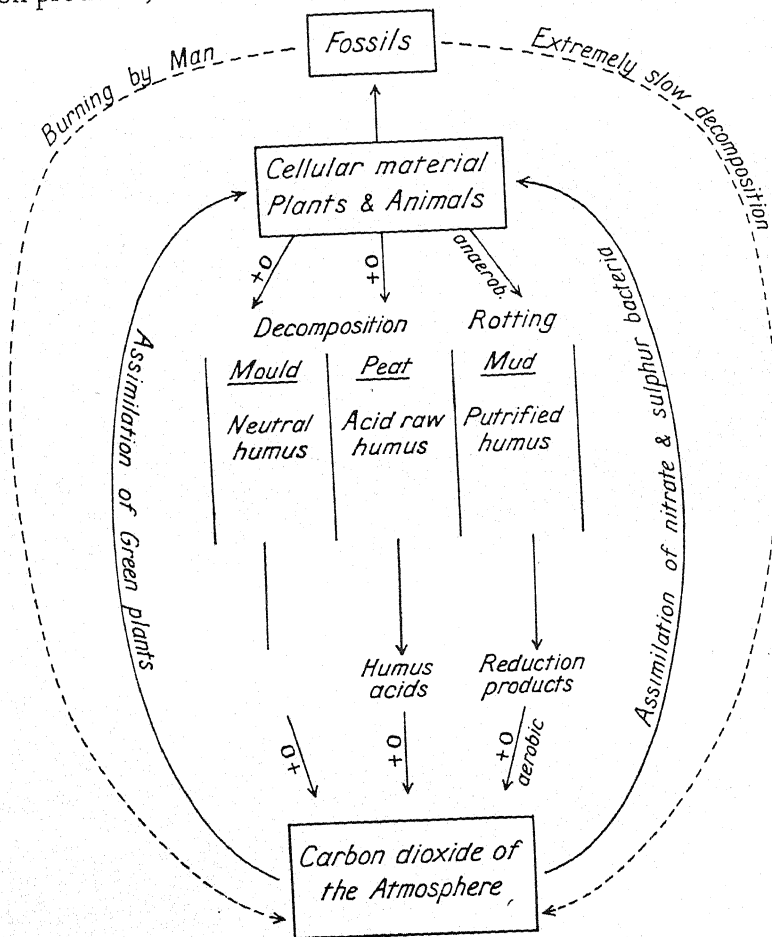
FIG. 74.—Carbon cycle in nature.

aromatic compounds poor in oxygen are given off either as gases or in the water. All these products of incomplete decomposition arrive finally in some place rich in oxygen or nutritive materials, where they are broken down to simple inorganic forms. It is comparatively rare for any intermediate product of the decomposition of carbon compounds to remain stored in the soil.

The nitrogen balance in nature is held under completely different conditions from the carbon balance. In the atmosphere there is a thousand times more nitrogen than carbon dioxide, while the percentage of nitrogen in plants is much less than the percentage of carbon. In view of the very small amount of total nitrogen which takes part in the cycle, it is surprising, at first sight, how much of it is retained in the soil. The nitrogen exchange in the soil proceeds more slowly than the carbon exchange; and this results in a decrease of the C/N ratio; this difference is probably due to the great chemical inactivity of nitrogen. The assimilation of 1 milligram of nitrogen by *Azotobacter* necessitates the respiration of from 50 to 500 milligrams of sugar (Christiansen-Weniger, 1923; Linhardt, 1919). Moreover, the nitrogen-fixing bacteria are very sensitive as regards soil reaction and available salts, and consequently many soils fix very little nitrogen at all.

As a glance at the scheme shows (Fig. 75), a considerable proportion of the nitrogen cycle includes only the plant and the soil; whereas, in the carbon dioxide cycle (Fig. 74), the atmosphere forms an integral part of the whole cycle.

Although the details of the various nitrogen cycles have been very little investigated, several different courses can be clearly distinguished, which are determined by the nature of the soil, and which are of some ecological importance.

1. *Ammonia Cycle.* This is to be found in soils where no nitrification occurs. Ammonia, as ammonium carbonate, sulphate, or phosphate, is taken up directly by the green plant, and transformed into protein. An "ammonium soil" always contains very little calcium. It tends to have an acid reaction, since the continued absorption of ammonium by the plant leaves behind an increasingly greater concentration of anion in the soil.

2. *Nitrate Cycle.* Nitrate in the soil is rapidly used up, partly by the higher plants, and partly by algæ and certain bacteria, to be built into protein. Denitrification disposes of some nitrate, too, and part is leached out from the soil. A complicated equilibrium prevails around the nitrates, which is influenced by other characteristics of the soil, such as the amount of fresh organic material present. An important source of the nitrogen supply for plants depends upon the fact that many plants store nitrates unchanged in their tissues. Sooner or later some of this nitrogen returns to the ground and is available for other plants. It is worthy of emphasis that the facility with which nitrates leach out from the soil is of

decisive importance for the nitrogen supply of aquatic plants. Nitrogen must often be the limiting factor among their nutrients.

Nitrate soils tend to have an alkaline reaction, since the nitrate ion is very rapidly absorbed by the plant, while the
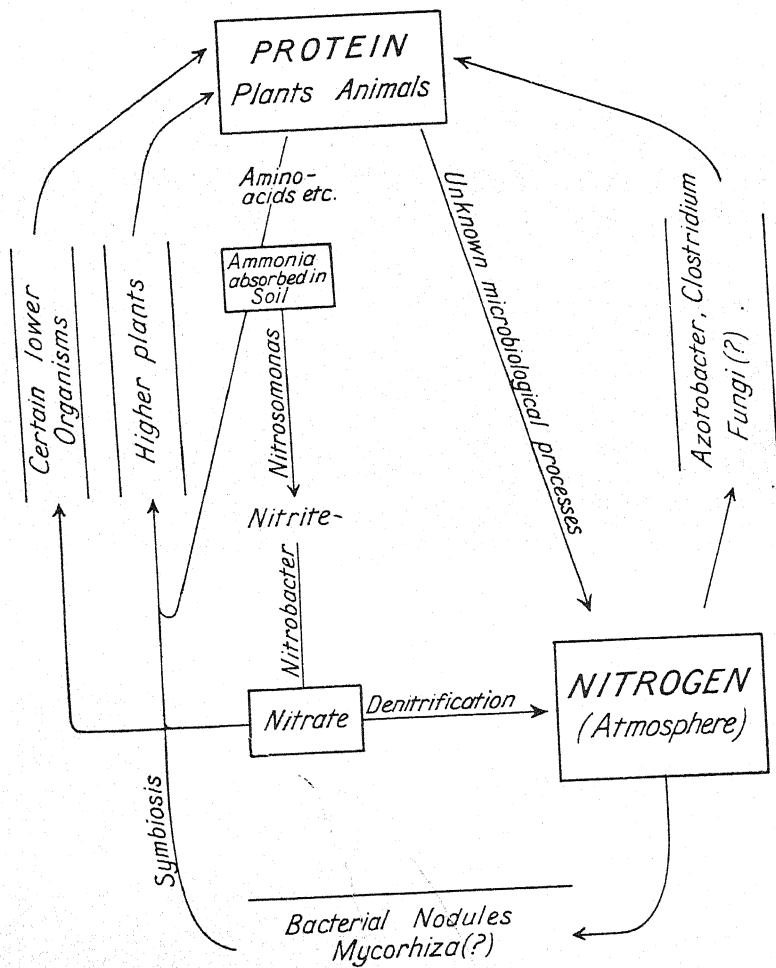
FIG. 75.—Nitrogen cycle in nature.

cation (often calcium) is more difficult to absorb. In nature the free calcium ions are combined anew as nitrates, and so the cycle proceeds without interruption.

For certain plants nitrite itself can serve as a nutrient (Kellner, Treboux, 1904).

3. *The "Complete" Nitrogen Cycle* is probably not entirely absent from any soil, but its relative importance must vary within wide limits.   Our knowledge is at present very incomplete upon this subject.   Nitrogen is stored up in the bodies of the soil micro-organisms, to appear again as ammonia upon their decomposition.   Where the micro-population of the soil is high, there will doubtless exist some competition between higher plants and micro-organisms for the available nitrogen, though there is no evidence as to how serious this competition is.   The death of micro-organisms throughout the year liberates the nitrogen for the use of higher plants.

The study of the population of the soil reveals a wonderful harmony of events, and a complex interdependence of micro-organism and higher plant.   Any change in the one calls forth a change in the other, and both are subject to climatic and edaphic conditions.

CHAPTER IX

THE CARBON DIOXIDE FACTOR[1]

CARBON dioxide is the only nutrient material of ordinary green plants which is derived from the air. Since 40 per cent of the dry weight of a plant is carbon, while the total ash content reaches only a few per cent, it is clear that carbon dioxide is absorbed in far greater quantities than are the inorganic materials of the soil. The study of the carbon dioxide economy of plants, therefore, is of the greatest importance, and until recently, has not received very serious attention. Before we enter upon a discussion of the distribution of carbon dioxide in nature we must know something of the relation between the concentration of carbon dioxide and the rate of photosynthesis.

1. THE PHYSIOLOGICAL ACTION OF CARBON DIOXIDE

Below a concentration of 1 per cent, carbon dioxide has no harmful effect upon living plant cells; at higher concentrations than this the gas begins to be toxic. It is only in the soil that such high concentrations are reached, so that in nature only roots, seeds, and soil organisms are liable to be so affected. In the atmosphere and in water, where the concentration is relatively low, carbon dioxide is merely a source of nutrient.

Many investigators have shown that the relation between assimilation and concentration of carbon dioxide is similar to that between assimilation and intensity of light (Blackman and Smith, 1911; Warburg, 1919; Lundegårdh, 1921, a; 1927, a; Harder, 1921). The important fact has been established that under normal conditions of illumination, the normal amount of carbon dioxide in the air (about 0·03 per cent) tends to limit the rate of assimilation. Figures 76 and 77 illustrate this point.

By increasing the light intensity falling upon the sun plant

[1] For a fuller list of citations concerning the subject-matter of this chapter the reader is referred to Lundegårdh, 1924, a.
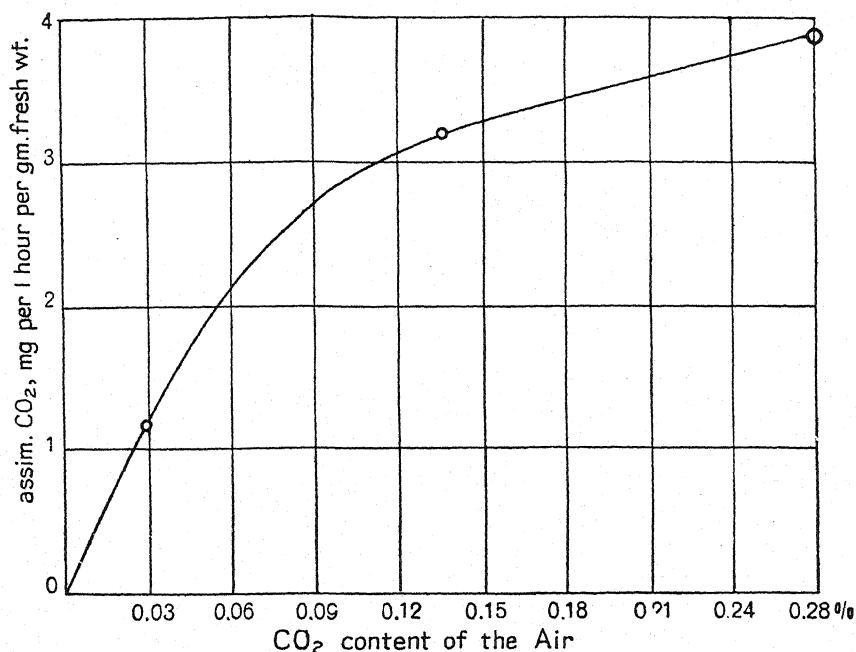
FIG. 76.—The relation between the photosynthesis of pine leaves and the carbon dioxide concentration of the air. (After Stålfelt, 1924.)
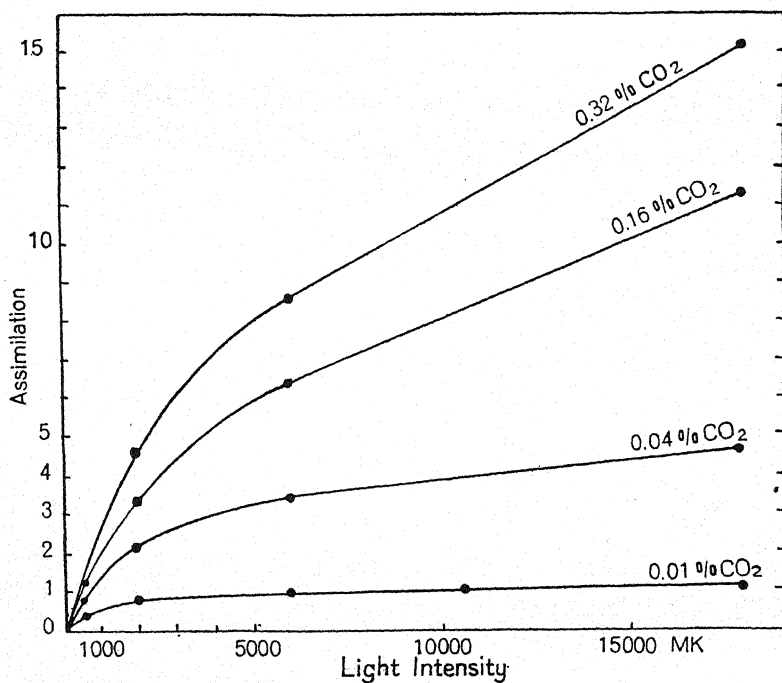
FIG. 77.—The relation between the photosynthesis of a water plant (*Fontanalis*) and the light intensity and carbon dioxide concentration. (Harder, 1921.)

Nasturtium palustre to three times its former value, the assimilation is approximately doubled; a similar increase of the carbon dioxide content of the air, at constant light intensity, results in a trebling of the assimilation. Similar results have been obtained by the author (1928) for other plants. Under normal light intensities, therefore, a sun plant is more sensitive to variations in the carbon dioxide content of the air than to variations in the light intensity.

Shade plants, too, are markedly dependent upon the carbon dioxide concentration of the habitat. We have already seen from Chapter II that the assimilation-light curve of shade plants becomes almost horizontal at a relative light intensity of about one-tenth. That is to say, that under normal concentrations of carbon dioxide an increase in the light intensity will not bring about any increase in the intensity of assimilation; though an increase in the concentration of carbon dioxide engenders a roughly proportional increase in the assimilation (Lundegårdh, 1921, *a*; 1924, *a*, pp. 80, 85). In shade plants, therefore, other conditions being optimal, and at light intensities above about 1/10 sunlight, the assimilation is almost exclusively controlled by the carbon dioxide factor.

Even at weak light intensities, when light tends to limit the process, a change in the concentration of carbon dioxide is effective. The work of Benecke (1921), Lundegårdh (1921, *a*), and Harder (1921), and of others has revealed the same general relationship here which has already (p. 29) been given the name of the "law of relative effects" of assimilation. When the light is in minimum—the natural conditions under which shade plants grow—assimilation is controlled more or less equally by light and carbon dioxide. It is obvious, then, that both sun and shade plants are influenced by the concentration of carbon dioxide around the assimilating leaves; and many glass-house experiments have demonstrated that an increase of carbon dioxide causes higher assimilation, an increased growth rate, and consequently a greater capital of carbohydrate (*see* Lundegårdh, 1924, *a*, 1927; 1928; Reinau, 1928).

In assessing the action of carbon dioxide, the other factors which influence uptake of carbon dioxide must also be taken into account: temperature, for example, stomatal movement, and the uptake of salts. When carrying out carbon dioxide manuring in closed green-houses, the temperature is particularly important. Figures 29 and 30 show that at a higher temperature the increase of assimilation due to heavy manur-

ing with carbon dioxide is much greater than at a lower temperature. Indeed it has been shown that the "efficiency" (the ratio: increase of yield/increase of carbon dioxide content) is much greater in warm green-houses than in the open air, where the mean temperature does not exceed 18° or 20° C. The addition of carbon dioxide to the atmosphere shifted the optimum temperature of assimilation from 20° to 31° C. for potatoes, from 19° to 36° for sugar beets, and from 30° to 36° for beans (Lundegårdh, 1928).

We have as yet no idea of the part played by the carbon dioxide concentration in the rate of assimilation of the autotrophic bacteria, sulphur bacteria, etc. Like the water plants, these organisms absorb carbon dioxide directly in the dissolved state. At all events, the part they play in the carbon dioxide cycle is very insignificant.

TABLE XLV

CARBON DIOXIDE CONTENT OF THE ATMOSPHERE IN THE SUMMER. (SOUTH SWEDEN.) 1920–6

	1920	1921	1922	1923	1924	1925	1926
CO_2 content—							
Mg./lit. .	0·612	0·5603	0·5267	0·5565	0·6189	0·5794	0·5935
Vol. %. .	0·03295	0·03031	0·02843	0·03000	0·0331	0·03125	0·03200
Temperature °C.. . .	19·1	17·3	16·5	15·4	16·4	—	—
Maximum var. % . . .	75·6	90·0	108·9	77·6	60·4	106·1	61·7
Mean var. %	—	16·1	15·2	14·4	21·0	7·1	9·4

In the soil, carbon dioxide occurs in much higher concentrations than in the atmosphere. Researches with the seedlings of higher plants have shown that when the carbon dioxide of the soil atmosphere rises above 1 per cent, the growth of the roots of the more sensitive species such as wheat, begins to decrease (Lundegårdh, 1923, b). So long as the content is not too high, the growth is just generally slowed down; at higher concentrations a decided poisoning sets in. It is difficult to say whether this poisoning is a direct consequence of the action of carbon dioxide, or whether it is due to secondary chemical processes in the soil. It has, however, been determined that an excess of carbon dioxide in the air is

definitely poisonous. Plants differ very much as to their susceptibility, and it is significant that most bacteria and fungi are more resistant than higher plants to increased concentrations of carbon dioxide, and are stimulated by concentrations of several per cent.

Fellows (1928) has produced evidence to show that *Ophiobolus graminis* is scarcely affected by concentrations of carbon dioxide as high as 18 per cent.

2. Carbon Dioxide as an Ecological Factor

The total content of carbon dioxide in the atmosphere is estimated at 2,100 billion kilograms; but the concentration is
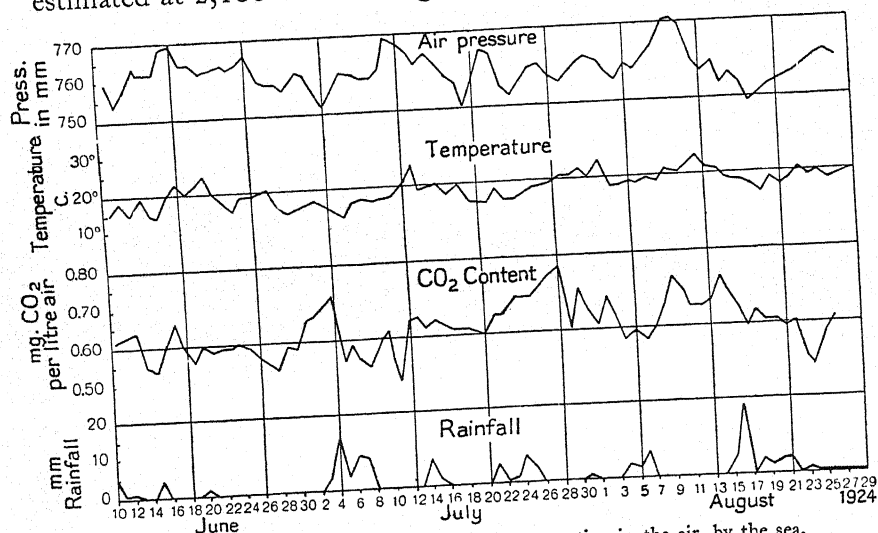
Fig. 78.—The daily course of carbon dioxide concentration in the air, by the sea, in the summer of 1924. Determinations at the ecological station at Hallands-Väderö.

very small, averaging about 0·03 per cent by volume, or 0·57 milligrams per litre of air. The concentration in the layer of atmosphere over vegetation is not constant, but varies within wide limits. Daily analyses carried out by the writer at the ecological station at Hallands-Väderö gave a mean variation of ± 9·4 to ± 21·0 per cent of the average values, in the summers 1921 to 1926. The maximum variation can reach as much as 100 per cent. Similar results have been obtained by Reiset, Selander, Letts and Blake.

These enormous variations in the carbon dioxide content can well be understood, since the total carbon dioxide content of the atmosphere is at most only thirty-five times bigger than

the annual "turnover" in nature; and daily fluctuations in the assimilation and the soil respiration (the two poles of the carbon cycle) are of significance (Fig. 78). Recent observations have shown that there is an undoubted correlation between the carbon dioxide content of the atmosphere, and factors, such as light and rainfall, which determine the intensity of assimilation and of carbon dioxide production in the soil.

The concentration at night, when the assimilation is suspended, is always higher than in the daytime. At 6 p.m. in a sugar-beet field, the mean concentration of carbon dioxide was 10 per cent higher than at midday. Annual fluctuations in the carbon dioxide content, too, can easily be traced back to the periodicity of assimilation and soil respiration. In autumn, for instance, the concentration of carbon dioxide increases
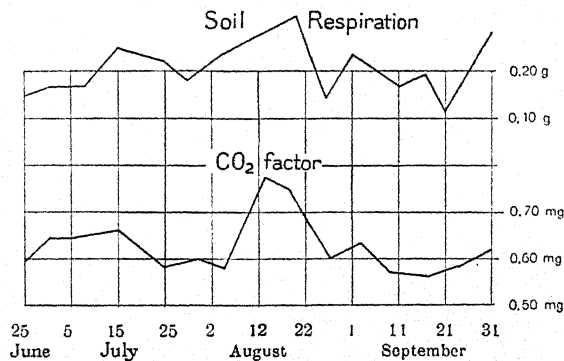
FIG. 79.—Seasonal changes in the soil respiration and the carbon dioxide factor, 1925. (Lundegårdh.)

simultaneously with an increase in the activity of soil bacteria, and a decrease in the assimilation; and in spring the concentration sinks on account of the vigorous assimilation. This annual variation is well illustrated in Figures 79 and 80. The two curves show the relation between the production and consumption of CO_2 in the year 1925. The "CO_2 factor" is the relation between the CO_2 content in the neighbourhood of the leaves and that in the air above, and is expressed as a percentage of the standard value in the air. It will be observed that the minimum value of the CO_2 factor is reached in July at a time when the assimilation is very high. The effect of soil respiration upon the CO_2 content of the air near the soil is evident from the parallelism of the two curves. From year to year, too, the content in the air changes (Table XLV). At Hallands-Väderö, in the summer of 1920, the concentration

was 0·03295 per cent, and in 1922 only 0·02843 per cent. Still greater fluctuations have been observed by Levy in the neighbourhood of Paris.

The annual fluctuations of carbon dioxide content may be correlated with the climate. After rainy summers, a high value is generally to be expected, since humidity favours soil respiration, while the attendant cloudiness decreases the assimilation.

In the oceans of the world is dissolved four times as much carbon dioxide as is contained in the atmosphere. As the partial pressure of the carbon dioxide in the atmosphere is reduced, a corresponding amount is liberated from the sea;
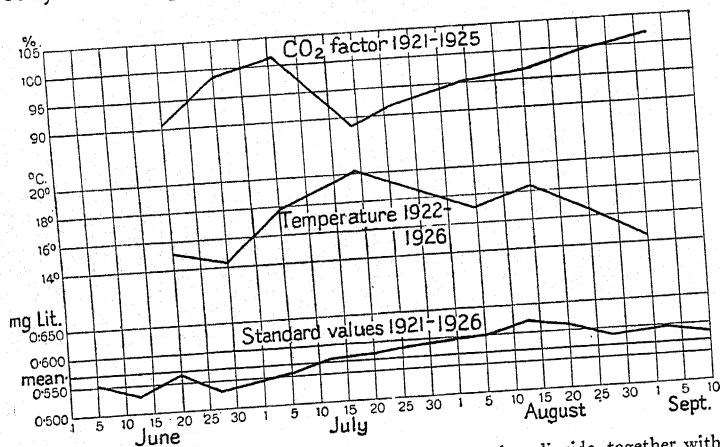
FIG. 80.—Mean curves for the standard values of the carbon dioxide, together with the carbon dioxide factor and the temperature, 1922-6. (Lundegårdh.)

and, as the partial pressure increases, a certain amount is dissolved in the sea again.

Since water plants, as a rule, can utilize directly only the free carbon dioxide in the water, and not the dissolved carbonates, the relative concentration in the water is higher than that in the air. It has been calculated, for example, that fresh-water lakes contain 40 per cent more available carbon dioxide than the atmosphere; and in the sea the active concentration is probably still higher, though data have not yet been presented on this point (Lundegårdh, 1924, *a*, p. 111).

The mechanism of uptake of carbon dioxide is simpler in the case of aquatic organisms, since the "air phase" in transportation of carbon dioxide to the chloroplasts disappears. According to calculations of Schroeder (1924), and Romell

(1927), the "hydrophase" of gas transport (its passage through the imbibed cell walls and the cytoplasm) offers 4·5 times as much resistance as the "air phase" (the passage through the stomata and intercellular spaces). However this may be, differences in carbon dioxide concentration will significantly affect the growth of aquatics (Fig. 77); and such differences occur not only at different depths, but in stagnant water over different areas of the same sheet of water, according to the constitution and the rate of decay of the soil beneath. The luxuriant algal flora in foul water which is rich in organic matter, is certainly due partly to the influence of carbon dioxide. No intensive research upon this interesting problem has yet appeared.

Let us revert to the land plants, and attempt to follow the carbon dioxide cycle in more detail. First of all, estimate must be made of the amount of carbon dioxide combined, and the amount given off every day. ·

A field of oats combines every day by assimilation about 13·3 lb. of carbon dioxide per acre per hour; and the soil respires about 4·5 lb. per acre per hour. In the bright hours of the day, therefore, there arises a deficit of carbon dioxide round the plants; a fact which has very often been demonstrated. This deficit engenders a vertical diffusion gradient, which brings about a downward flow of carbon dioxide from the air above.

In summer there is a daily period of assimilation of about eight hours; this will result in a total deficit of $8 \times 8·8$ = about 70 lb. per acre. A volume of air 100 metres high, over one acre, contains about 490 lb. of carbon dioxide. If, in the course of eight hours, all this quantity were equally accessible to the plant, the assimilation of the field of oats would reduce the carbon dioxide concentration of the air by about 15 per cent. In the field much greater deficits are often measured, so that it may be assumed that the atmosphere at the disposal of the plant does not extend to 100 metres above the field. This will depend upon the abundance of the vertical air currents, for the amount of carbon dioxide brought down by diffusion is very small. If the flow of air is horizontal, and is over wide stretches covered with vegetation, there will be very little replacement of carbon dioxide.

The facts outlined above, together with a mass of similar data, lead to the conclusion that the atmosphere is only a *reservoir* of carbon dioxide, and is only directly available to a

limited extent for vegetation. Plants derive the greater part of their carbon dioxide from the ground layers of the atmosphere, and the prosperity of the plant is controlled by a narrower carbon dioxide cycle between the plant and the soil (*see* Fig. 81). The wider cycle between the plant and the atmosphere is a reserve upon which the plant can draw if the narrower cycle is insufficient, a reserve which is very variable on account of currents in the atmosphere.

The calculations given above concerned only the balance of
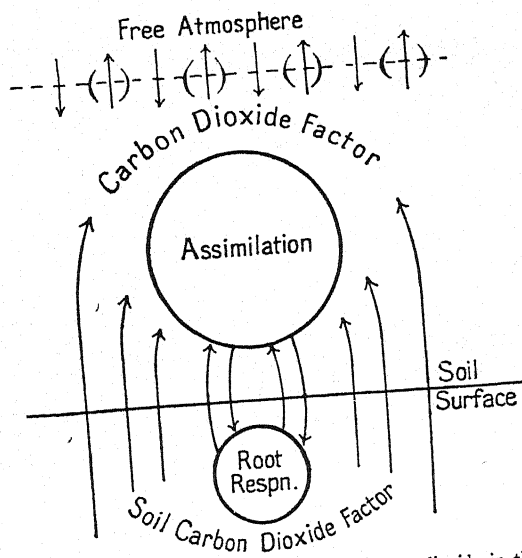
FIG. 81.—Diagram to illustrate the movement of carbon dioxide in the vegetation layer. When photosynthesis is intense, the carbon dioxide respired from the ground is insufficient, and the reserve in the "free atmosphere" is drawn upon. Under such conditions, the minimum concentration of carbon dioxide is in the region of the leaves.[1] When photosynthesis is weaker, some carbon dioxide is returned again to the free atmosphere (arrows in brackets).

carbon dioxide during the daylight. During the night a great deal of carbon dioxide is given out by the soil into the atmosphere, so that the deficit formed during the day is made up. In the example given the plants used up during the day $13.3 \times 8 = 106.4$ lb. of carbon dioxide, and in the whole of 24 hours the soil yields $4.5 \times 24 = 108$ lb. So, even if there is scarcely any horizontal movement of the atmosphere, the plants are amply provided with carbon dioxide. Through the wind, the concentration of carbon dioxide in the atmos-

[1] The occurrence of this minimum has been confirmed by Reinau (1927) and Keuhl (1926).

phere is equalized over wide areas of high and low carbon
dioxide consumption. The writer has shown that in woods,
in spite of a vigorous soil respiration, there is often a negative
carbon dioxide balance (Lundegårdh, 1921, e; also Meinecke,
1927; Romell, 1928). The following figures give an idea of
the respiration of different soils:

TABLE XLVI

SOIL RESPIRATION IN VARIOUS HABITATS

Soil.	Respiration lb. per acre per hour.	
Clay (not manured)	1·1	Lundegårdh
Sand (not manured)	1·8	,,
Sand (not manured, rich in humus) . . .	3·57	,,
Loam (not manured)	3·54	,,
Loam (rich in humus)	3·67	,,
Forest soil (beech)	13·7–19·6	,,
Forest soil (alder)	10·5–20·0	,,
Poor meadow soil.	2·95	,,
Forest soil (acid humus)	2·1–5·4	Romell

Carbon dioxide is only drawn from the atmosphere above
the plant layer, when the respiration of the soil does not provide
sufficient of it, and a diffusion gradient is set up. When the
carbon dioxide is in excess, the diffusion gradient is reversed,
and carbon dioxide is returned into the upper layers of the
atmosphere; and under these conditions, the vegetation
depends entirely upon the soil for its supply of carbon dioxide.

The soil respiration can be measured by isolating a portion
of the soil surface under a bell jar, and determining after a
certain time the amount of CO_2 which has accumulated
(Dönhoff, 1927; Romell, 1928, et al.). Since the soil respira-
tion varies from day to day, and during the year, no reliable
values can be obtained without a series of readings.

In making measurements of the carbon dioxide factor of
any habitat, it will be necessary, on account of temporary
variations, to make a whole series of observations. The
method employed should have an accuracy of at least 5 per
cent of the normal content of the air, i.e. about 0·025 milli-
grams per litre (Lundegårdh, 1922, c; 1924, f; 1924, a,
p. 10). The apparatus is described in Figure 82. It is

usually sufficient to make one estimation per day, at the time of most vigorous carbon assimilation, between 9 a.m. and 11 a.m. From a series of at least thirty analyses a practicable mean value can be derived. In dealing with the carbon dioxide factor, the mean values are perfectly good measures, for the assimilation, under normal conditions of the atmosphere, is more or less proportional to the amount of carbon dioxide present.

For a more exact estimation of the effective carbon dioxide concentration in nature, it is not sufficient to take measurements from one *level* of the plant alone. There is always established a diffusion gradient between the upper and lower leaves of the plant, so that the lower leaves are usually in a higher carbon dioxide concentration than the upper leaves. Unfortunately, such a series of analyses at different heights is very tiresome to obtain; and although they would give a satis-
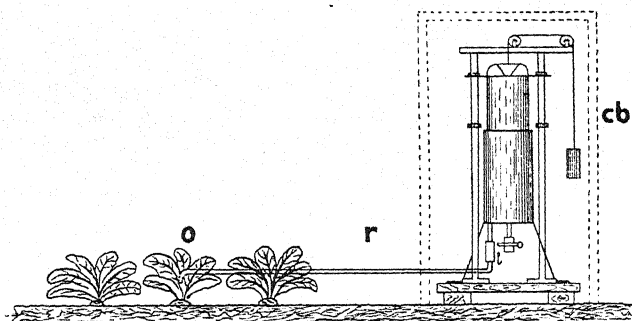
FIG. 82.—Apparatus for the determination of the CO_2 factor in nature. On the right is the "bell glass" in a protecting case. r is a glass tube bent down at the tip over the leaves.

factory idea of the distribution of carbon dioxide, their value is diminished owing to the great error in measuring the assimilation among the lower leaves of a plant. For ecological purposes, the writer is of opinion that determinations of the amount of carbon dioxide immediately above the topmost leaves of a plant, gives a sufficiently accurate result. In formations of several "strata" of plants, determinations must obviously be taken above each stratum; such determinations have been made by Romell (1928) and Féher (1927). The factor, when obtained, can be expressed either in absolute units—in milligrams per litre of air, or in volume per cent— or in relative units, i.e. the percentage of the concentration in the air at some distance from plants.

An investigation of the carbon dioxide factor in different habitats has given the following results:

1. In an unmanured cultivated field of cereal or beet, the carbon dioxide factor is always negative, i.e. less than the normal value. The writer has found a deficit of 41·7 per cent.

2. After fertilization with farmyard manure and especially a complete artificial manure, or a combination of the two, the soil respiration is raised, for the salts stimulate bacterial activity, and the carbon dioxide factor increases. Under favourable conditions it becomes positive; in the writer's experiments, values of + 20 per cent were reached (Lundegårdh, 1924, a, p. 224).

3. The factor in natural meadows varies according to the constitution of the soil and the vegetation. Both positive and negative values of the factor have been measured. When the soil is damp and rich in humus the value is often positive.

4. In woods the carbon dioxide factor at the level of the smaller herbs is almost always positive; on account of the high respiration of the forest soil, combined with the low assimilation rate of the under vegetation. In a *Viola palustris, Oxalis acetosella* association, on the floor of a damp elder and beech wood, values as high as + 254 per cent have been observed. Three feet above the soil level the concentration had fallen to 147–170 per cent; and at the height of the tops of the trees, negative values of the factor were obtained. In woods, therefore, there is a fairly steep concentration gradient, a phenomenon correlated with the vertical extension of the vegetation.

In fields the gradient is steeper. Between the upper and the lower leaves of a potato plant, differences of 30 per cent have been found.

5. In the lowest layers of vegetation, among mosses and algæ, very high values of the carbon dioxide factor are to be expected; and in caves too, high concentrations occur.

The increasing gradient of carbon dioxide toward the soil in woods provides some compensation for the parallel decrease in light intensity. On account of the higher concentration of carbon dioxide the plants in the lower layers are better able to endure the shade, and to make use of the sun flecks which cross them from time to time.

A determination of the soil respiration per unit area of soil, though an indirect method, will give some idea of the intensity of the carbon dioxide factor. Some plants, such as the extreme shade plants, are found to prefer soils with a high

respiration, and these may be regarded as "carbon dioxide plants." The carbon dioxide factor is essentially an edaphic factor, though it depends in addition upon the air currents, height and thickness of vegetation, and so on. It is evident that a determination of the soil respiration gives only a first approximation to the real carbon dioxide factor, though it is most practicable for the ecologist.

The measure of the soil respiration is also of value in determining the total "earning rate" of the plant. In cultivated fields, the carbon dioxide respired from the soil is often parallel to the yield of the crop (Lundegårdh, 1924, *a*, p. 271; 1928). In natural soils, too, a high soil respiration bespeaks a vigorous nitrification. In agriculture generally, the carbon dioxide factor is of considerable importance, since it has been shown that carbon dioxide is generally a "limiting" factor, and that over unmanured soils, the concentration may be only subnormal. The agriculturist must give his full attention, therefore, to any process which aims at increasing the carbon dioxide production of the soil. First importance should be attached to fertilization with mineral salts, since they simultaneously serve as direct nutriment for plants, and as a stimulus to bacterial activity. Farmyard manure acts more slowly, since it introduces fewer available salts into the soil; though there is in its favour its ability to break up the ground well and to maintain the humus content. A mixture of natural and artificial fertilizer is obviously most satisfactory. Cultivation is also advantageous, since it loosens the soil, and it is important to keep up an equable humidity. The vigorous respiration of a forest soil is probably to be attributed to the combination of humidity and looseness of structure. On both these questions, irrigation and the mechanical cultivation of the soil, the last word has not yet been said. The observation of soil respiration will be a useful test in the trying out of new culture methods. It should be emphasized that the absolute humus content of the soil in no way regulates the intensity of carbon dioxide production. There is a limit, probably very small, below which the humus content cannot sink without endangering the rate of carbon dioxide production. Soil respiration depends primarily upon the intensity of the activity of micro-organisms, and this intensity is principally determined by the presence of nutritive salts (Fig. 83).

Finally it should be mentioned that soil respiration cannot increase indefinitely without causing harm. Activity of

micro-organisms is principally restricted to the upper 30 centimetres of mould, where the aeration is still very good, and the carbon dioxide escapes by diffusion. Other things being equal, an increase in the soil respiration produces a corresponding increase in the carbon dioxide concentration of the air above the soil. Even when the soil respiration is low, as in an unmanured field at a depth of 15 centimetres, the concentration of carbon dioxide in the soil can be ten times
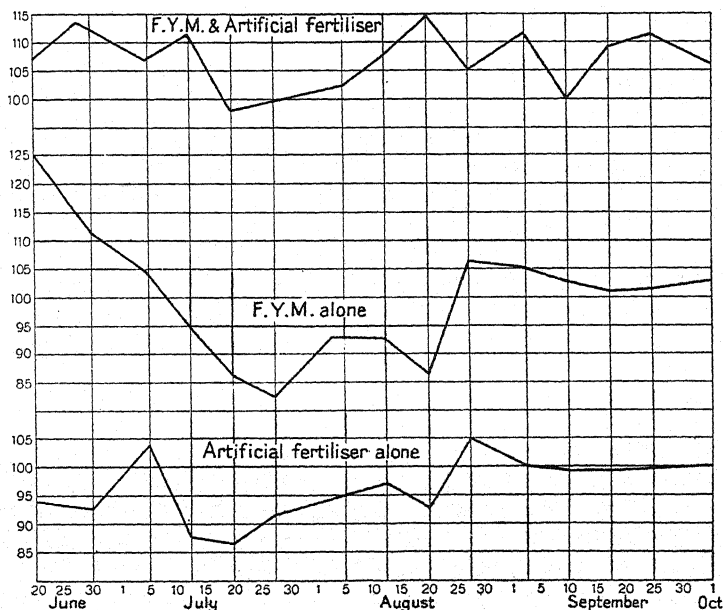
FIG. 83.—The behaviour of the carbon dioxide factor in three differently manured fields. The curves are the means of six annual experiments. The ordinates measure carbon dioxide (100 the standard value). Only when both farmyard manure (F.Y.M.) and artificial fertilizer are applied together does the carbon dioxide concentration remain above the standard value. The curves show also the course of the carbon dioxide factor through the vegetative period. The depression at mid-summer, at the time of highest assimilation, is very striking.

higher than the concentration of the air, i.e. as high as o·30 per cent. A trebling of the activity in the soil, under these conditions, will bring the concentration almost up to 1·0 per cent, which is the lower limit of toxicity.

There is a limit, therefore, to the amount of carbon dioxide fertilization which is practicable. The concentration above the soil must not be permitted to rise as high as 1·0 per cent. Indeed, as soon as the concentration is so high that carbon dioxide is diffusing out into the atmosphere, the practical limit has already been reached.

T

CHAPTER X

PRINCIPLES OF EXPERIMENTAL ECOLOGY

THE preceding chapters have presented the leading contributions to experimental plant ecology, and to causal plant geography. It remains briefly to emphasize the principles and points of view of this research, and to estimate its significance in such studies as floristics. Let us consider first the species concept in ecology.

The Linnæan species is an abstraction, since no two individuals, no two phenotypes, are exactly alike. But this abstraction certainly rests upon a basis of reality, namely, the pronounced discontinuity of organic forms. The species is a group within which there occur numerous "transitions" between individual forms, but which is more or less clearly cut off from other species groups. When discontinuity in nature is not absolute, it is impossible to distinguish the species sharply from one another. In many genera the determination of species is easy, since transition types are extremely rare; in other instances the whole genus is a chaos of fluctuating forms, which graduate indistinguishably into one another.

The species concept, then, can never be an exact one; the species is an approximation, and there will always be controversy among systematists over "critical species," where the boundary between species and form is mobile.

At the outset we must inquire what is the cause of this relationship, whereby the wealth of organic form can be separated into groups (species) which so often exhibit such pronounced discontinuity among one another. Systematists, cytologists, and geneticists have disputed endlessly over this problem, without reaching any clear issue. The problem will only be considered here in so far as it has a bearing upon the subject of this book.

From the geneticist's point of view, there are neither species nor forms, but only series of genotypically identical individuals, described by Johanssen as "biotypes." To the

geneticist a Linnæan species is a population of biotypes which hybridize freely among themselves, but rarely hybridize with other groups of biotypes. As is well known, the crossing of species scarcely ever succeeds, though there do occur species which admit of hybridization (Jones, N. W., 1922; Heribert-Nilsson, 1918; Åkerman, 1921; Winge, 1926). Presumably there is a definite *relationship* among species; why hybridization should take place more easily in one case than in another is a physiological problem which has not yet been solved. The low fertility of interspecies crosses may depend upon several causes. There is a constitutional opposition to fertilization and the setting of seed; furthermore, only those crosses which prove themselves efficient in nature survive in the vegetation at all. It is, as a matter of course, quite conceivable that only when similar biotypes are crossed is there prospect of a large number of viable combinations. If the parents are very dissimilar in their genotypic constitution the prospect is smaller that a "harmonic" combination will result. In the geneticist's garden an almost unlimited number of biotypes can be produced by crossing. In nature, however, the number of distinct forms is very limited, a fact which may be ascribed to the stringency of natural selection. Clausen (1922) has shown that among his biotypes of *Viola tricolor*, there are 5,308,416 possible combinations ! The taxonomist Wittrock has described only 40 "microspecies" in nature.

Up to the present the geneticist has worked almost exclusively with morphological characters. Now it is improbable that these characters play as vital a part in survival as physiological characters; and of the selection of physiological characters we know very little. Euler has discussed the chemical differences between closely related forms (1929). It is the task of experimental ecology to discover the characters "chosen" by selection, that is to say, the most "appropriate adaptations," and to investigate these quantitatively. Ample evidence has already been adduced for the importance of such characters as specific intensity of assimilation, shape of the assimilation curve, intensity of respiration, osmotic pressure of the cell sap, resistance to desiccation, and so on. It may well be assumed that physiological characters are often linked with morphological characters, and the latter will therefore appear to be selected, though they are not primarily chosen out in the struggle for existence. Characters such as flower

colour, shape of corolla, and the detailed form of the foliage
leaves are for the most part of little value to the plant ecologi-
cally; though they may serve the ecologist a useful purpose
in distinguishing for him different ecological forms.

Enough has been said already to show that the species
concept is largely conventional.[1] In ecology, the Linnæan
species is useful to survey roughly the enormous number of
plant types on the earth, and to classify them into superficially
indistinguishable units, which are no more real *units* than the
atoms of physics. The value of this classical division of
living forms can certainly be rated highly, but such a division
should not and cannot be regarded as the final goal of taxono-
mic analysis. This has been realized by systematists them-
selves, and species have been split up into varieties (known
as "micro-species" by Ostenfeld, 1921; "isoreagents" by
Raunkiaer, 1918; and "Ökotypes" by Turesson, 1922).
For the ecologist this further dissection is of immense value.

Experimental ecology has advanced from the consideration
of climatic conditions in general, and their bearing upon
plant formations, to the analysis of the climatic and edaphic
factors over a very small area. Concomitant with this there
has been a refinement of physiological methods, which at
their best are able to determine the smallest differences in the
functional life of the individual. For such work the Linnæan
species is too coarse a unit. Since the fundamental discoveries
of Johanssen, physiology has worked with pure lines; and in
experimental ecology the same principle should be observed.
Modern agriculture has furnished some excellent examples of
the different ecological behaviour of closely related biophytes,
and it is well known that the systematic "forms" of a species
often prefer very different habitats. Any flora will furnish
examples of this; and examples are given by Drude (1913)
and Münch (1923). Turesson has recently isolated similar
"forms" from many wild plants (1929), and Beljakoff, in the
present writer's laboratory, has established marked differences
in the assimilation curves of different strains of barley.

It is at this point that a difficulty appears. Very rarely
does there spread in nature a single isolated biotype. The
species is generally not a biotype, but a complex of them.
Nor is the microspecies usually an isolated biotype, but a

[1] For recent literature on the species concept, the reader is referred to Lotsy
(1916), Plate (1914), Diels (1921), Shull, G. H. (1923), Winge (1926), Turesson
(1929), Heribert-Nilsson (1928), Robson (1928). (The Species Problem) [Ed.]

smaller complex of nearly related biotypes. Only in those exceptional cases when the plant has propagated itself homozygously could one speak of an "isogenic" propagation; in fact only clones, i.e. plants reproducing themselves apogamously, like *Hieracium* and *Erophila*, can be said to be isogenic (Bannier, 1923). All other plants spread, as a rule, as heterogeneous populations; by hybridization and by mutation there arise from this population new biotypes, from which, by selection, the fittest for the particular habitat are allowed to remain permanently. (*See* Cajander, 1916; Turesson, 1922, 1925; and Clausen, 1922.)

The question arises next as to whether selection ever goes so far as to eliminate all but a genetically pure or almost pure form. There is as yet insufficient evidence available to give a decisive answer to this question. From the relatively small number of real micro-species encountered in nature, compared with the number theoretically possible according to Clausen's estimate on p. 275, it can be gathered that selection is very severe. This is especially the case in unfavourable habitats. It might quite well be, that at the limits of propagation of a species, selection has reduced it to a single biotype, which remains as a stable homozygous form. But within the natural area of a species, conditions are obviously favourable for a multitude of micro-species.

It is possible, too, that some forms of a species are able to disseminate themselves better than others. Turesson (1922) found that the different micro-species of *Hieracium umbellatum* (a forest form, a dune form, and a form growing in sandy soil) occur in pure colonies all over their respective habitats, though in the transition zones a number of intermediate forms were to be found. This can be explained on two hypotheses: either the whole population moves, and the specialized forms are always being differentiated anew in the several specialized habitats, or, the various micro-species migrate on their own account, but can only develop properly in their appropriate habitats. In nature probably both processes occur: the migration of a complex population, and its differentiation into various forms, and the migration of stable forms themselves. The facts advanced by Turesson: that the coast forms of *Hieracium umbellatum* differ on the east and west coasts of Scandinavia; and the facts advanced by Clausen: that the forms of *Viola* differ in a similar way along the coast of the North Sea, favour the first of the two alternatives given above.

According to the modern idea, then, systematic "forms" are selected by ecological factors from a population of species. At the basis of this idea is Darwin's selection theory, which assumes a vigorous variation within the species. To-day, owing to the rapid development of genetics, we are in a better position to appraise the nature of variations. Variations consist of mutations (of whose nature very little is known) and crosses from which new stable types are constantly arising. The weakness of Darwin's theory lies in his somewhat nebulous concept of variation: it was identified by Korschinsky (1901) and de Vries (1901–04) with the discontinuous variations known as mutations. More recently the mutation hypothesis has been to some extent replaced by the concept of hybridization as the cause of the origin of new genotypes. Indeed, Heribert-Nilsson has shown that variations can be accounted for without the need for mutation (1918).

Naturally there clings much that is hypothetical to this modern idea of selection. But it is capable of experimental verification. If there is a continual selection of forms from a population of species it can be followed directly in the habitat where the succession of vegetation still occurs. Ecology still awaits research of this sort, critically and statistically performed.

The fact of the general *fitness* of plants to the environment is accepted almost as an axiom. On account of the severe competition between individuals for room and nourishment, specialization is often carried very far indeed—a condition analogous to that in human society. The phenomena of adaptation would certainly be very remarkable, were organic forms not subject to variation; in fact, the only explanation would be the teleology of the older botanists. In the light of modern genetics, however, there is no doubt that new forms— micro-species—are always arising. Only those micro-species which are adapted to the local environmental conditions remain; the others disappear. It follows from this, that the number of micro-species in a species is never constant. In artificial culture, under optimal conditions, where every plant has enough room for its full development, an enormous number of micro-species develop; but even under favourable conditions in nature the number is markedly reduced. Moreover, a change in the climatic conditions will bring forth other micro-species. In such a way the course of evolution becomes intelligible (Cajander, 1921; Turesson, 1924).

Now if the origin of micro-species is an ecological process, it is easy to understand how species which are widely separated taxonomically can assume a similar "life form" (in the sense of Warming and Griesbach), which is then clearly recognized as an adaptation to the conditions of the habitat. Examples of such life forms are to be found in the "cactus form" (*Cactaceae*, species of *Euphorbia*, and *Stapelia*), the "Nymphaea form" (*Nymphaae, Hydrocharis,* and *Limnanthemum*) and dune forms (such as *Carex arenaria, Agrostis stolonifera, Elymus arenarius,* and *Triticum junceum*). It is quite unnecessary to explain this morphological convergence, as Vesque (1882) and Warming (1909) tried to do, by an appeal to direct Lamarckian adaptation.

The Lamarckian conception of life forms has arisen from an obscure presentation of the mechanism of adaptation. The transplantations of Kerner, Bonnier, Lesage, Massart, Schmidt, and others showed a marked "adaptation" of the transplanted plant to some other climate, or to different soil factors. Were one to transplant perennating plants, and were these to show changes in the new shoots, one could be certain that a phenotypic adaptation had taken place. When seeds are sown, on the other hand, one is probably dealing with genotypically heterogeneous material; and without a genetic analysis it is impossible to decide whether there has been a real phenotypic adaptation, or whether nothing more than a selection of types has taken place. The work begun by Turesson, which aims at defining the boundary between phenotypic and genotypic adaptations, promises important results. According to the results which Turesson has already obtained, it seems that genotypic adaptations play the more important part in the existence of the plant, though phenotypic adaptations do occur, and cannot be distinguished superficially from genotypic adaptations.

This bearing of experimental ecology upon the problems of phenotypic adaptation is one of the most important questions confronting us. From the results of plant physiology we know that the plant possesses an astounding plasticity, and that its modifications are for the most part "suitable" ones. The preceding chapters provide abundant illustration of this: the adaptations of sun and shade leaves, etiolation, regulation of osmotic pressure, root production, and colour in the *Cyanophyceae*. This plasticity of the plant is without doubt an extremely important complement to genotypic variation,

since plasticity guarantees a continued dissemination of the plant under changing external conditions. In no instance have the modifications proved to be absolutely "heritable," though it is known that the influence of a modification can extend to the subsequent generations as a gradually diminishing "after effect." A great deal of work has been done to bridge the cleft between modification and genotypic adaptation, but the work has not yet yielded any result (Semon; Sperlich, 1919). The possibility of such a relation is, however, too important to be dismissed without consideration.

The "suitability" of modifications, like the "suitability" of fixed genotypic life forms, varies within wide limits (see p. 85). One should not judge from morphological appearances alone. The practice up to the present of subdividing life forms according to their outward appearances has, in certain instances—that of the xerophytes, for example,— proved to be very misleading. The author has often advocated the need for a classification of adaptation forms upon a physiological basis. The next few pages will be devoted to a description of the method of physiological classification.

For the ecologist, the habitat is the standard, and the plant world should be regarded from this standard. This view was adopted by Warming, and in the English edition of his work (1909) he has outlined a classification of adaptation forms according to the predominating ecological factors.

It is the endeavour of research in experimental ecology to separate the real "adaptation forms" from forms defined by purely taxonomic criteria, to distinguish those characters which turn the scale in the struggle for existence from those which are of purely secondary importance. Naturally there is no attribute of the plant which is completely unimportant from the ecological standpoint; but characters which are of the greatest importance in taxonomy are often quite subordinate in ecology.

The principle of Selection cannot explain all forms and types. In the very nature of living substance there lie basic principles of evolution, capable of a causal explanation. These are, perhaps, somewhat analogous to the crystal laws, and are produced by the complex interplay of myriad organic factors. Selection cuts out a number of these forms, as totally unsuitable; but many are allowed to survive, all equally suited to the environment, though differing among themselves widely in morphological form.

An example of morphological divergence with ecological similarity is given by the northern conifers and certain deciduous trees which flourish together in the cold-temperate regions of Scandinavia. Here the same ecological problem—the cold winter—is overcome in two ways. On the one hand, there is defoliation and a "cold-resistant" resting phase, coupled with intense carbon assimilation in the summer; on the other hand, there is a perennial "cold-resistant" foliage, coupled with a weak absolute intensity of assimilation.

In making any classification it must be remembered that ecology has to deal primarily with "competition forms" (oligophytes), forms which have arisen in the course of severe and continuous selection, and whose habit and function can be regarded as weapons against the dominant ecological factors. The various competition forms will receive their names from these dominant factors. Warming, for instance, has divided plants into hydrophytes, eremophytes, lithophytes, halophytes, and so on. Within each "competition group" there are a number of forms, ecologically identical, but exhibiting great morphological divergence. Among the hydrophytes, for example, there are "cormus" and "thallus" forms, with thread-like, branched or unbranched vegetative bodies.

From the ecological standpoint, the critical factor is the factor in minimum or in extreme superabundance. According to the "law of relative effects," the minimal factor has the greatest relative influence upon growth. When the geographical distribution of a plant is correlated with some definite factor, the limits of distribution will be quite well defined when that factor is in minimum. A similar influence is exerted by a factor so much in excess as to be inhibitory. Figure 84 serves as an illustration of this. This curve represents schematically the action of most factors which affect the activity of plants. Such a curve can be analysed, as Blackman analysed his time-respiration curves, into a rising and a falling component. The optimum is that part of the curve immediately after which the inhibitory factor begins to operate. The *relative* influence of a factor, which determines the boundaries of a flora, has no appreciable magnitude at the optimum value of the factor. At this region of the curve, the factor x can vary considerably, without effecting much change in the relative influence, y. In Figure 84 the relative influence of the factors is represented by the shaded areas,

and the effects of successive variations of 10 per cent in the factor have been depicted. When the factor is in the minimum region the percentage variation in the function is nearly equal to the variation in the factor. As the factor increases in intensity the corresponding increase in the function becomes smaller and smaller; until the factor reaches supra-optimal values, when its effect rapidly increases again.

If it is assumed—and it is a very plausible assumption—that the plant can only function satisfactorily within a certain range of variation, then the risk of a factor overstepping this range will be greatest in the minimal and supra-optimal regions of its action. A plant, therefore, at the extreme limit of its geographical distribution will be most sensitive to variations in soil and climate.

One difficulty in the classification of adaptation forms occurs, when two or more factors interact in affecting the plant. Often the influence of two minimum factors is united: e.g. water shortage and salt shortage in poor sandy soils. Sometimes a minimum and an inhibitory factor occur together, as in arid salt soils, where a shortage of water and a super-abundance of salts occur together. In such instances the introduction of sub-groups is of advantage. Xerophytes, for instance, are divided into halophytes and oligotrophytes, the latter group including plants growing on poor sandy soils.

The introduction of such sub-groups enables one to classify the finer differences in vegetation under more localized climatic conditions. Series of types, progressively less and less influenced by the ecological factor in minimum, can be constructed; for example, the halophyte series would begin with extreme "salt plants," and would end with steppe plants, where the content of salts is only just above the optimum content. A similar series, of xerophytes, would begin with desert plants, and pass through semi-desert types, steppe types, rock vegetation in the temperate zones, to chalk vegetation. This classification follows more or less the general curve of factor influence given in Figure 84.

At the beginning of every series of forms, therefore, stand the ecological "competition forms" (oligophytes); and at the end are to be found the mesophytes—under which definition are included those plants in the series which grow in the most favourable habitats. *Absolute mesophytes*, in the sense of non-competition forms, include those plants whose geographical distribution falls within the optimum range of all the factors.

There is indeed no paradise for plants on the earth, but as the next substitute there are the tropical rain forests. At the opposite end of the scale there are the polar regions; and plants in these regions might be described as extreme oligophytes. The more "oligophytic" a vegetation is, the easier it can be split up into adaptation forms; and the more mesophytic a vegetation, the more difficult is it to include in the classification. Mesophytes are the "critical forms" of ecology.
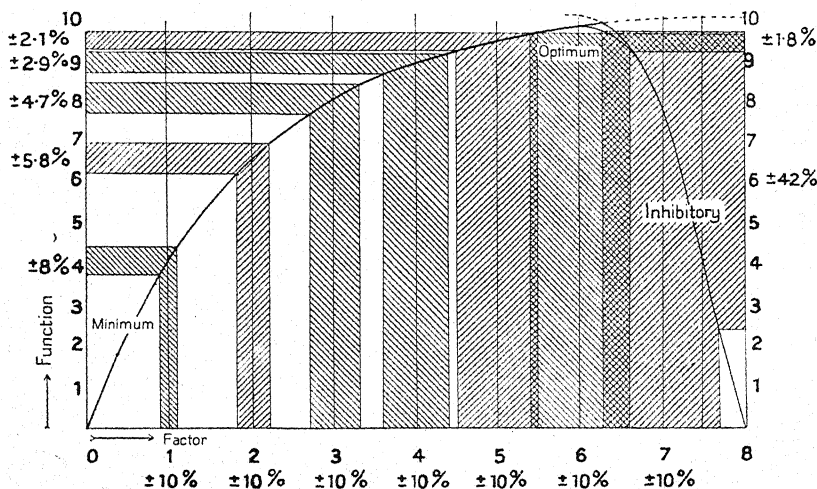
FIG. 84.—Schematic representation of the biological law of relative effects. The rising curve, produced into a broken line, illustrates the case in which the function continuously increases; and the shaded columns represent variations of 10 per cent in the factor. The corresponding horizontal areas represent the relative action of the function at different absolute values, and it will be observed that the relative effect of the factor decreases as its absolute value increases. The optimum curve can be resolved into a rising curve and a rapidly falling curve; and this latter curve corresponds to the inhibitory action of the factor at higher intensities. The relative effect of the factor is insignificant in its optimum region, and increases rapidly in the minimum and especially the supra-optimal region.

Oligophytes will naturally occur in mesophytic habitats as pioneers of the vegetation, subsequently to be driven out by other plants. The habitat which a plant will endure is really determined by its "ecological amplitude." Referring again to Figure 84, we can postulate two plants, one of which will function within a variation of 20 per cent of the controlling factor, while the other will only function within a variation of 10 per cent. The former plant will obviously survive extremes of the particular factor better than the latter. Differences in distribution of plants may depend on differences in their "ecological amplitude." One plant might exist between the

limits 2 and 6 in Figure 84, while another might grow between the limits of 1 and 7. It is clear that the law of relative effects throws much light upon the distribution of plants, an aspect of ecology suitable for experimental investigation.

The following survey of adaptation forms makes no claim to completeness, but should rather be regarded as a short summary of the results described in the preceding chapters. It is scarcely necessary to call attention to the fact that we are scarcely launched into this subject. However, the reader will find that, in certain aspects, the following classification is an advance upon previous classifications.

Survey of Adaptation Forms

Note.—For brevity, adaptation forms are indicated by "Ad." The separation of the action of factors into "periodic" and "more continuous" facilitates a more rational distribution according to climatic zones.

I. Water Factor.

A. Xerophytic Adaptations. Water factor in Minimum.

(*a*) *Uniform dryness.* Desert plants. Ad.:—great capacity for resistance against changes of water content in the tissues; reduction of transpiration; protection against insolation; high osmotic pressure; high root pressure; deep roots; intracellular carbon dioxide cycle. The adaptations themselves can be subdivided. Thus, succulents of the cactus type usually possess a low cell suction pressure, while other types have an extraordinarily high pressure.

(*b*) *Periodic dryness. Annual Periods.*

(1) Plants in the arid and semi-arid regions of steppes, tree steppes, savannahs, maquis, and in part, prairies. Ad.:—short vegetative period; ability to stand desiccation; xeromorphy of the aerial parts; deeply penetrating roots, resistant resting organs; and sometimes water storage in the stem.

(2) Mediterranean vegetation. Ad.:—evergreen vegetative organs, with winter assimilation period.

(3) Inhabitants of Arctic ice deserts.

Shorter Periods.

(4) Rock Plants. Ad.:—resistance against frequent and extreme desiccation; absorption of water through the

whole vegetative body. Real rock plants include only lichens, certain mosses, and certain algæ.

B. HYDROPHYTIC ADAPTATIONS. Water Factor in "excess."

  (*a*) *Continuous life in Water.* (Hydrophytes.) Ad.:— Hydromorphy of the vegetative organs and of the reproductive cycle; gas exchange with the water; chromatic adaptation.

  (*b*) *Periodic Submersion.* The inhabitants of periodically dried-out bogs, or periodically flooded regions. Mosses, like *Sphagnum*, and species of *Hypnum* and *Amblystegium*. Flowering plants, such as *Hottonia palustris*, *Oenanthe aquatica*, and in the sea, *Spergularia salina*, and *Glyceria maritima*. Ad.:—The gas exchange of these plants can be carried on as well in water as in the air; though the details of this relationship have not yet been worked out. The gelatinous sheath protection of algæ in the littoral zone might serve as a protection against periodic desiccation. Some flowering plants form two sorts of leaves; in others, the vegetative period is suspended in times of drought, and the life of the plant is carried on through resting organs.

  (*c*) *Bog Plants.* (Helophytes.) Ad.:—accommodation of the subterranean organs to poverty of oxygen in the substratum.

II. Temperature Factor.

  (*a*) *Continuous high and low temperatures.*

      (1) The flora of hot springs. Ad.:—a high assimilation optimum, and a high thermal death point.

      (2) Algæ in the polar seas, and snow algæ. Ad.:— low assimilation optimum, and protection against the freezing of the cells.

  (*b*) *Periodic Temperature Changes.*

      (3) "Cold-loving" and "heat-loving" plants in neighbouring habitats. Ad.:—in the former, low, and in the latter, high temperature optima for various processes; in the former, high, and in the latter, low suction pressures.

      (4) Alpine Plants. Large daily variation in temperature; low night temperatures. Ad.:—very low assimilation minima and respiration optima (Senn, 1922); adjustment of growth according to the Alpine conditions (Senn, 1922); high osmotic pressure; plagiotropic growth of shoots and leaves.

(5) Polar Plants. Large annual variation in temperature, very low winter temperatures. Ad.:—very short vegetative period; very low temperature minimum of growth; extreme protection against freezing out of the cells (and probably a low level of the assimilation optimum).

III. Light Factor.

(a) *Differences in Light Intensity.*

(1) Plants growing in darkness. Flora of the soil, and deep sea; certain parasites, Fungi and Bacteria. Ad.:—heterotrophic metabolism; negative phototropism of the vegetative stage.

(2) Extreme Shade Plants (Dämmerungspflanzen). Vegetation at great depths in the sea, etc.; algæ and liverworts in woods and in caves. Ad.:—very low compensation point; chromatic adaptation, very low dry weight.

(3) Obligate Shade Plants. Zone of the lower brown algæ in the sea, etc. Ad.:—low compensation point; "flattened" shape of the assimilation curve; high chlorophyll content; low dry weight per unit leaf area; shade leaves; low-lying shoot system.

(4) Facultative Shade Plants. (Helio-sciophytes.) Juvenile forms in weak light; adult forms in full light. Ad.:—great plasticity of the leaf type, etc.

(5) Sun Plants. Upper levels of the sea; land formations. Ad.:—logarithmic shaped assimilation curve rising to a high level; "sun leaves"; tall shoot and leaf system frequent; pan- or a-photometric leaves.

Alpine plants, and certain sea-shore plants, are extreme types of sun plant; and in these plants special adaptations probably occur. Thus in some Alpine plants, such as *Arnica montana*, growth is not affected by high light intensities (Senn, 1922); *see also* Lloyd (1921). As general rule, light, when very intense, does inhibit growth.

IV. Nutritional Factors.

(a) *Autotrophic Plants.*

(1) Oligotrophic Plants. Plants growing in situations where all food materials are in minimum. Includes moorland plants, many acid humus plants, plants growing on sand and boulders, and some rock plants. Ad.:—

slow growth, i.e. economy in the vegetative period; vegetative period covering as long a time as possible; woody stems and roots which store salts. This group includes evergreen trees (conifers), "semi-bushes" (*Erica-ceae*), rosette plants, lichens, and mosses with unlimited growth such as *Sphagnum.*

(2) Eutrophic Specialists. Nitrate plants, and to some extent lime plants, nitrophilous lichens, etc. Ad.:—resistance against the high concentrations of certain ions.

(*b*) Heterotrophytes.   Saprophytes and Parasites.

V.   Chemico-Physical Factors.

(1) Halophytes. Ad.:—marked regulation of suction pressure; resistance against high concentrations of certain ions (chlorides and sulphates), excretion of salt in certain instances.

(2) p_H series, "alkali plants" (to which group belong certain lime plants), "neutral plants," and "acid plants." Ad.:—unknown, possibly electric charges on the cell walls and in the plasma.

VI.   Character of the Substrate.

Edaphic Adaptations in the Narrower Sense.

(1) Rock Plants.

(2) Chasmophytes, growing in rock clefts. Ad.:—perennating rosettes or cushions, often with tap roots.

(3) Plants on moving soil; on dunes and sometimes on loess; sand and mud soils by the sea or by flowing fresh water. Ad.:—horizontal creeping rhizomes or roots; geophilous shoots, etc.; a pliable growth habit; effective seed dispersal; many weeds of cultivated fields belong in this class.

VII.   Plants in Wind-exposed Habitats.

Ad.:—prostrate growth forms—plagiotropic shoots; rosette or cushion types; well-developed torsion strength of the stem (e.g. Cocoanut palm), or of the halm in grasses; sclerenchyma in the leaves (*Phoenix, Dasylirion, Phormium,* etc.); includes coast and desert forms.

VIII.   Ecological Specialists.

Plants which have evolved along peculiar lines as regards their growth forms or their nutritional relationships.

(1) Lianes. Ad.:—Twining or climbing shoots.

(2) Epiphytes. Ad.:—Absorption of atmospheric humidity through the vegetative body in mosses and lichens, or through special organs such as the aerial roots of orchids or the leaves of *Bromeliads*; arrangements for collecting humus, as in *Platycerium*.

(3) Insectivorous Plants. Ad.:—arrangements for entrapping and digesting insects.

(4) Semi-parasites. Arrangements for the extraction of food, and especially water from host plants (Kostytschew, 1922; Tubef, 1923).

(5) True Parasites. Wholly heterotrophic way of life, at the expense of the living plant; adaptation for attacking and plundering the hosts.

(6) Symbiosis. Linked by many transitions to the parasites. Occurs in the following combinations: bacteria and bacteria; bacteria and algæ; algæ and fungi (to form lichens); bacteria and higher plants; fungi and higher plants (in the form of mycorhiza).

The last three groups together can be considered as "food specialists," since parasitism and symbiosis presuppose a very specialized type of nutrition. Since the metabolism of bacteria and fungi is so very varied, it is scarcely surprising to find parasitism and symbiosis occurring so frequently in these groups. From the despoiling of dead bodies to the attacking and despoiling of the living is only a step; in fact, there are examples of facultative saprophytism and parasitism in the same fungus or bacterium. By a process of selection, parasitism would easily arise from saprophytism.

As has already been mentioned, this enumeration of the most important adaptation forms is no more than a rough outline of a classification according to ecological characters. Enough examples have been given to demonstrate that, even in extreme types, several adaptation forms are united in the same biotype. Very often, for example, xerophytic and thermic adaptation forms, and adaptations to strong winds, are combined in the same individual. Such instances might be multiplied. A continuation of this method of analysis will finally enable the botanist to set up a complete system—a "key" of plant life in relation to ecological characters.

Within the limits of the survey given above, account has not been taken of the "biotic" adaptations; i.e. those adaptation forms which have arisen as a result of the proximity and

competition of other plants. There are undoubtedly a great number of such adaptations—symbiosis is only a special group among them—and they have received less attention than the climatic and edaphic adaptations. In many instances even purely physiognomic observation is lacking. For example, there is very little data upon the mutual struggle of the subterranean parts of plants for their position in the soil. Plants are probably adapted for this competition by both morphological and chemical methods. Perhaps the phosphatides which are passed into the soil by exosmosis (described by Hansteen-Cranner) play some part as defence against rivals. Upon this point scarcely anything is known. Nor do we know with certainty whether the "soil fatigue" known to agriculture, after repeated cultivation, depends upon the separation out into the soil of plant poisons. The "soil fatigue" can be cured by heating or by treatment with lime. The poison, whatever its nature, acts in aqueous soil extracts (Grafe, 1922). Among the lower organisms, for example, "self poisoning" by the products of their own metabolism is well known, though these products, under certain conditions, stimulate growth (Nikitinsky, 1901; Küster, 1909).

This competition for space among organisms is naturally more intense and severe, as the climatic and edaphic conditions are better. Biotic adaptations, therefore, occur more frequently among mesophytes; though it is questionable how many of the characteristics of mesophytes are really to be regarded as adaptations. Among mesophytes, in many instances, it is the form of the plant which assigns to it its place in the society. The more favourable the conditions of a habitat, the greater is the play for climatic and edaphic adaptations—witness the wealth of forms in a tropical rain forest. The earliest plants to become established occupy the ground, and soon spread into a closed formation, where the individuals are distributed in a mosaic according to the biotic factors; but whether the life forms are *selected* in favourable habitats, seems very questionable. Those plants which cannot be accommodated in the more favourable, find accommodation in the less favourable habitats, and it is in these habitats, in the struggle against nature, that the most "efficient" forms are selected. According to this conception, mesophytes represent a reservoir of mixed ecological forms, heterogeneous as to their genotypes, which constitute a source for the origin of new biotypes.

On account of this struggle for space, plants are often obliged to spread into habitats which are less favourable to them as regards the climate and soil. Alders, for instance, grow luxuriously in well-aerated ground, but they are crowded out by other trees. In Madeira, *Vaccinium madeirense* grows best in the laurel "maquis"; but it is seldom found there, while it is very common in higher and less favourable regions (Warming, 1909, p. 367). In culture, out of the way of competition, heather will thrive on rich lime soils; in nature its occurrence is generally accounted an index of the poverty of the soil (Schröter, 1923, p. 222). Certain "salt specialists," particularly the halophytes, are most widely distributed in salty soils, only because they succumb to competition in other places. A superficial observer would include the ferns among shade plants. But ferns grow in woods, not because they are shade plants, but because they need a high humidity, and they prefer a combination of high humidity and full light intensity (Seifriz, 1924).

PLANT SOCIETIES

A complete taxonomy of life forms from one standpoint is scarcely possible. A purely morphological division of forms can certainly be carried on indefinitely, but such a division has very restricted value, since it brings into one group plants which grow in very different habitats, and which are therefore not geographically related. The method which has been adopted here—the classification of competition forms adapted to the minimum or the inhibiting factor in the environment, has this advantage: that it is of use in the interpretation of the geographic distribution of plants over wide areas. There is no doubt that the geographical distribution of plants reflects accurately the interplay of ecological conditions; so that an ecological classification, on the basis of the selection theory, should be of fundamental value.

It is in dealing with the mesophytes that this scheme breaks down. The action of climatic factors and of the soil is less prominent than the action of the plants upon one another. The environmental factors are in the neighbourhood of their optimum values, and experimental analysis is rendered so difficult that the whole idea of "adaptation forms" becomes very nebulous. In a mesophytic community, quite a large variation in some factor will have relatively little influence upon the vegetation. This accounts for the fact that

mesophytic plant societies are often very stable and are found in places whose climate and soil differ markedly. Failure to recognize the consequences of this law of relative effects in ecology has led certain plant geographers to the false assumption that plant societies can be independent of the ecological conditions.

The genesis of a plant society is a process stretching over a long period of time. Only in very few regions of the earth is it possible to observe the colonization of new areas: in the Arctic, for instance, on sea coasts, and in volcanic regions. The experimental study of succession has received attention from the American school (Clements, 1916), but progress has not yet been carried very far. In the progress of succession, the number and the kind of seeds, and the constitution and changes in the climate and soil, are of decisive importance.

Pioneer plants reproduce themselves very rapidly, and by forming a closed covering over the ground, often prevent the germination of other seeds which might have taken an important place in the society. The plants themselves take part in the formation of the soil; the type of mineral weathering and aeration of the soil depends upon the type of humus they form. The accidental arrival of certain plants upon new land, therefore, can lead to the development of the soil in a definite direction, and the succession will set out upon a definite road. In many regions, the development of the vegetation hesitates between moor, wood, and meadow, and it is almost impossible to determine the ecological factors which have resulted in the establishment of moor over one stretch, and woodland over another. Indeed, in many instances, the vegetation is determined by the nature of the pioneers.

There arise very striking divergences in the constitution of plant societies when geographic or biotic barriers stand in the way of the immigration of a flora. Mountain chains are well known to form such barriers, and even other plant communities can be serious obstacles to colonization. Palmgren has shown in Åland (1921) that a stretch of water, no more than a kilometre broad, forms an important vegetation barrier. According to Palmgren, the immigration of the Åland meadow flora has taken place from Central Sweden. In Western Sweden there are 299 species, and in the east only between 200 and 234. The immigration, therefore, is not yet completed. From the researches of Palmgren and other

workers, it can be concluded that the colonization of a region may extend over thousands of years.

The development of a plant society is never fully complete. The climate is always changing in one direction or another, new species are always immigrating, and new forms arising. In Scandinavia it has been possible to follow the migration of plant societies to and fro, from post-Arctic times, by drawing up "pollen diagrams" along the main "plant trails" (Walter, 1927).

The present flora cannot be regarded as any more than a static representation of a dynamic evolutionary sequence; and from the extended migration of an individual species, no information can be obtained as to whether the centre of distribution was really the ecological optimum. For these and many other reasons the ecological classification of mesophytic societies is very unsatisfactory.

Those plants which have been described as oligophytes, on the other hand, are more closely related to their habitat. The length of time during which the habitat has been evolving is therefore of subsidiary importance, and it is possible, with some certainty, to deduce the nature of the climate and the soil from the character of the vegetation. Even in more mesophytic societies, where the soil is heterogeneous over a small area, and is covered by the same vegetation, it is usually possible to pick out the influence of environmental factors on the different layers of vegetation. In northern forests, for example, the ground vegetation has been used as an indicator of the quality of the soil for forestry (Cajander, 1909). It is well known to every observer that *Trientalis europea, Aira flexuosa*, etc., in northern forests are an infallible sign of raw humus, while *Anemone nemorosa*, and still more *A. hepatica*, also *Oxalis acetosella, Maianthemum bifolium*, etc., often indicate real mould soil. It is very instructive to follow from year to year fluctuations in small strips of vegetation, which result from fluctuations in the climate. It would be a mistake, however, to apply these observations to wide areas, where factors like colonization and migration really come into operation. In comparing two vegetation types, some distance apart, but within the same climatic zone, it is often discovered that an apparently similar soil is populated by different societies, and this can partially be attributed to the mode of colonization of the society. Problems such as these require great critical judgment and very thorough investigation to ascertain

whether the environment in the two habitats is exactly the same or not.

When migration and colonization are no more factors in the plant society, an equilibrium is reached which has been called by Clements a "climax." In the climax, every plant has attained the position and space which it can claim on a basis of its "vitality" (and under this somewhat vague conception is included growth, reproduction, and the ability of the plant to compete with its neighbours). If the ground were laid bare, and development could begin again from the beginning, then, if the climate remained constant, the same society would arise a second time. Such a regeneration can often be seen in forests, where stretches have been laid waste by fire; there is an immigration of species into the waste stretches from the neighbouring old formation. The temporary flora arising from seeds left in the ground, or from foreign communities, is gradually eliminated. Sometimes seeds from quite different regions in the same climatic zone are introduced and the advent of these might give rise to a totally different vegetation. A different vegetation will arise also if the soil or the climate is changed before colonization. Beechwoods, for instance, will not regenerate if the soil has begun to develop raw humus. If a beechwood is carelessly coppiced, it will degenerate into a grass formation with straggling bushes.

It is, on the whole, true, that the regeneration of a society, or the re-immigration of a species, will only succeed when all the conditions are favourable for propagation. In fact the degree of frequency of a species is an expression of the fitness of the environment for that species. "Relic" species subsist preferably in places where the ecological conditions approach most closely the original conditions under which the "relic" lived. The significance of "relics" is still very uncertain; they may, in fact, be the outposts of an oncoming migration.

In a plant society there is more than a mere co-existence of growing plants. Only in the most unfavourable situations are the plants isolated from one another; and in a closed formation they struggle against one another for space. As the free space on one horizon grows less, the formation extends vertically. Shallow-rooted and deep-rooted plants will grow well together (as in woods and in meadows), and sun and shade plants will flourish together also. A plant society, therefore, is composed of several adaptation forms. In the forests these fall into specific layers, which are determined principally by differences

in their adaptation to light: trees, bushes, herbs, and mosses. Moreover, when the soil consists of strips of raw humus and mould, or differs in water content from place to place, the ground vegetation changes. The subordinate associations in forests are more dependent upon the edaphic conditions than is the dominant association, i.e. that of the trees themselves. Since fluctuations of soil moisture occur in the upper layers of the soil, the shallow-rooted herbs are more affected than the deep-rooted trees.

Even in shallow formations it is possible to distinguish various associations of mosses, algæ, and herbaceous plants, either distributed in strata or adjacent to one another horizontally. In the latter case the differences in vegetation are due to edaphic factors—moisture, hydrogen ion concentration, aeration, nitrate content, and so on. There is still divergence of opinion as to whether these should be regarded as separate societies.

A discussion of the principles of plant sociology is outside the scope of this book; and for such a discussion the reader is referred to the excellent recent works of Walter and Braun-Blanquet. By the word association is commonly understood a plant society which has a definite floristic composition. Two societies of identical composition are, however, never encountered, so that the conception of association, like the species concept, is purely abstract.

The formation, in plant sociology, is analogous to the concept of genus, in that it embraces closely related associations. Neither association nor formation has any relationship to experimental ecology. To understand the development of a plant society requires a study both of the relative effects of the environmental factors in the society, and of the biotic factors such as migration and colonization.

In contrast to the climatic and edaphic factors, which are, on the whole, easy to define and to measure, the biotic factors are extremely complex, and can be unravelled only with difficulty. On the one hand, there is seed distribution and colonization, and on the other hand, there are those factors involving the mode of vegetative growth of shoots and roots, e.g. climbing plants, creepers, and so on. The influence of the plant on the soil can also be considered as a biotic factor. A species, flavoured by climatic conditions, can influence the soil in such a way that other plants are quite excluded.

When the biotic factors influence such properties as the p_H

of the soil, they become to some extent susceptible to measurement. But it is extremely difficult to express the general vitality and the competitive efficiency of a plant, and indeed the experimental investigation of such quantities has scarcely begun. In the province of plant sociology some attention has been paid to them, and it is the aim of such concepts as dominance, degree of covering, sociability, stratification, and so on, to deal with these vague biotic factors.

Plant societies can be divided into those which are homogeneous and those which are heterogeneous. A homogeneous society will occur only when the "controlling" factor acts over a wide area. Such a society will undergo a definite evolution until the climax is reached: the climax being in fact a condition of equilibrium between the migration, the colonization, and the biotic factors. Every significant change in the complex of factors starts the development on its course again, the magnitude of the change depending upon the relative influence of the changing factor. Information as to the degree of stability of the various societies can be obtained from careful statistical analysis, together with measurements of the known ecological factors. Observations over a period of years on one restricted region are of great value for this type of work.

In mixed formations, on the sea shore, or in bogs, there is often to be seen a zonation of the vegetation. As one retreats from the sea shore the water content of the soil decreases continuously, and there might be expected a corresponding *continuous* change in the aspect of the plant societies. Instead of this gradual change, however, there is generally a marked zonation. The vegetation occurs in strips, each strip dominated by some species. This zonation depends partly upon seed dispersal, for the seeds are deposited at different distances from the sea (owing to the changes in water-level through the year) and partly upon the conditions regulating the distribution of species within the association. A few species, particularly suited to the habitat, are dominant, and all the other species occur in a much lower frequency. It seems that as soon as a plant enters a habitat where it is out of its optimum environment, its frequency decreases rapidly; and for this reason the associations pass into one another quite sharply, since they are classified according to the dominant species. Near the sea, the water factor is in its supra-optimal range, and the vegetation is very sensitive to it, hence there arise zones of plants differently adapted to water. The zonation does not

indicate that the vegetation is determined by the edaphic factors alone, though if these are in minimum, they will exert a maximum effect upon the vegetation.

An enormous literature has grown up concerning the classification of natural plant societies. Almost every author in the realm of plant sociology has his own system, containing large numbers of technical terms. Hult (1881; 1885), Brockmann-Jerosch (1928), Rübel (1912), du Rietz (1921) and Brenner (1921) have all taken up the usual physiognomic viewpoint. The societies are named after their dominant species.

The purely floristic description of plant societies is certainly the first necessary step in every investigation in plant geography; and very often one is unable, at first, to go any further. This, however, is no reason for supposing that physiognomic plant sociology is an independent science. The vegetation of a habitat depends not only upon the climate and the soil of the habitat, but also upon biotic factors, and migration and colonization; so that it is not surprising that two identical habitats should possess totally different floras. This, however, is no argument against the basic principle of ecology, namely, that the vegetation is determined by the climatic and edaphic conditions. It is just such problems as these which encourage the application of the methods of experimental ecology to the sociology of plants. It is important to remember that the plants themselves take part in the creation of their own environment. Although this principle has been recognized for some time in soil science, sufficient account has not been taken of it in experimental ecology.

The factors of greatest importance in the composition of a plant society may be tabulated as follows :

A. FACTORS OF THE HABITAT.
    I. Climatic Factors.
        (a) Light.
        (b) Temperature.
    II. Factors involving both Climate and Soil.
        (a) Water.
        (b) Carbon Dioxide.
    III. Soil Factors.
        (a) Physical Structure of the Soil.
        (b) Aeration.

        (c) Content of Nutrient Salts.
        (d) Hydrogen ion Concentration.
        (e) Population of Micro-organisms.

B. BIOTIC FACTORS.
    I. Genotypic Plasticity of the Species in the Population.
   II. Phenotypic Plasticity of the Biotypes.
  III. "Vitality" and "Fitness in Competition" of the
       Individual Forms.

C. MIGRATION AND COLONIZATION FACTORS.
    I. Situation of the Habitat with regard to the Surround-
       ing Centres of Distribution, and to Plant Geo-
       graphical Barriers.
   II. Variety and Number of the Seeds entering the
       Habitat.
  III. Conditions of Colonization of the Plants.

D. HISTORY OF CLIMATE ON THE EARTH.
  The Nature and Direction of Gradual Climatic Changes.

    The groups A, B, and C fall within the realm of experi-
mental ecology, as it has been outlined in this book. Group A
we have treated in some detail. Group B, I, described by
Turesson as "Genökologie," is still in its earliest stages of
development, but promises interesting results. Group B, II,
is equally important. In the foregoing pages the wide
differences in the plasticity of plants have often been men-
tioned. In this branch of physiology a vast field of research
lies open.
    Group B, III, embraces a number of important biotic
factors, which are difficult to define, factors involving the
general vitality of growth and reproduction of the plant. The
weeds of cultivated fields, and Elodea, in the waterways of
Europe, are illustrations of plants in which the "vitality" is
high. Colonization by plants of such high "vitality" will
often divert the development of a plant society into a totally
different direction; and it is probable that the similarity of
different associations is often due to their having been
colonized to different extents by such forms. It is one of the
important tasks of experimental ecology to discover and to
enumerate the qualities which make up "vitality."
    Very little progress has been made in our knowledge of
Group C. Attention has already been called to the signifi-
cance of plant barriers, and to the velocity of plant migration.

Scarcely any exact experimental study has been devoted to seed dispersal. It would, for instance, be of great interest and significance to determine the number of seeds shed over a habitat in the course of a year; and to proceed to a study of the means of natural selection among seedlings. The influence of topographical factors, such as protection from wind, and the presence of water or snow, constitutes another problem of great interest (*see* Ridley,[1] 1930).

The phenomena included in Group D do not fall within the range of experimental investigation. The reconstruction of ecological conditions in geological time must depend upon our knowledge of the present relation between climate and vegetation. Some understanding of the greater climatic changes through time may be reached by a co-operation of the geology of the quarternary epoch and of experimental ecology.

It seems clear that the study of the complex of factors which determine the aspect of the earth's vegetation is of far greater importance than the enumeration of plant societies; and that the enormous amount of literature which has been published on the question of nomenclature represents work which could more profitably have been spent upon other branches of science. The classification of plant societies is a means and not an end in itself, and only when this point has been clearly understood will a practical nomenclature be discovered, which is neither too rigid nor schematic.

Since the environmental factors are only part of the complex which determines the composition of a formation and an association, classification must not include the environment alone. A statistical analysis of its floristics should always precede the description of a plant society. Such an analysis can be made according to the methods described by Fries (1919) or Raunkiaer (1909). By Raunkiaer's method, if the quadrat is divided into 100 small quadrats, the "degree of covering" can also be determined (Vallin, 1925; Lundegårdh, 1927).

The plants growing in an undisturbed simple plant society are distributed according to a simple law (Jaccard, 1902; Raunkiaer, 1918; Du Rietz, 1920; Palmgren, 1916; Romell, 1920–23; Kylin, 1923; Wicksell, 1924; Nordhagen, 1923) (Figs. 85, 86). A number of the plants, the so-called "constants" (usually between 10 and 30 per cent of the total

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[1] *The Dispersal of Plants throughout the World.* Ridley, H. N. 1930. [Ed.]

number of species), occur in the quadrats very often. These
are said to have a frequency of 90–100 per cent. The other
species are so divided that those of more rare occurrence have a
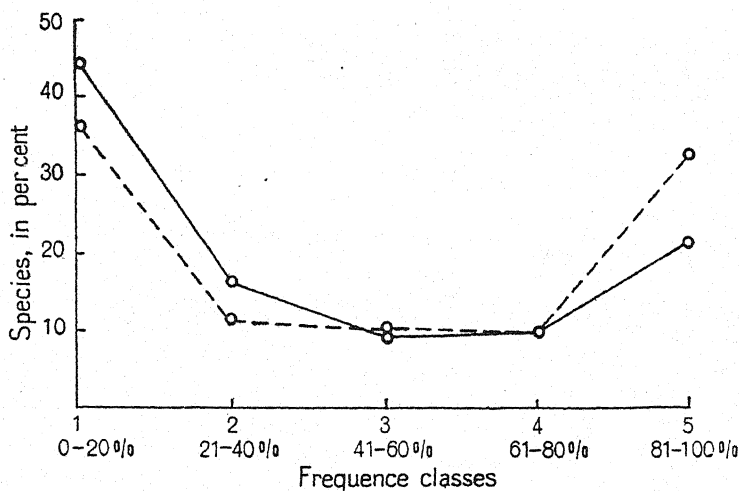
FIG. 85.—Frequency curve. (After Brenner.)
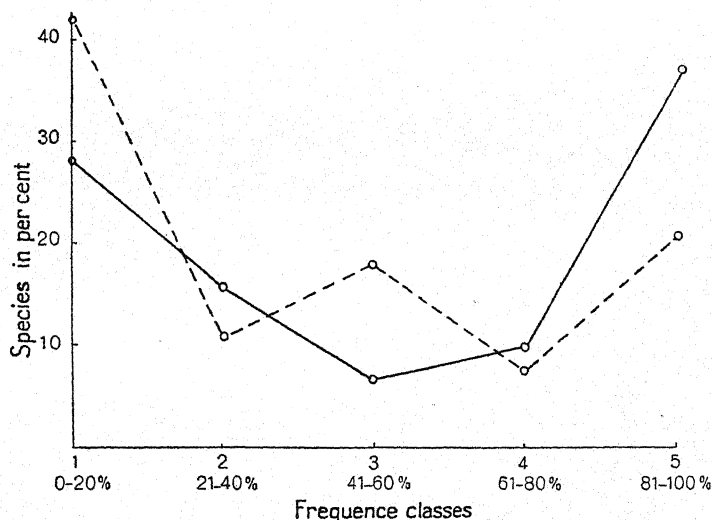
FIG. 86.—Frequency curve. (After Nordhagen.)

very low frequency, while those of intermediate occurrence fall
into intermediate classes. The curves obtained by these
methods are saddle shaped, since they have a maximum in the
highest frequency classes and a maximum in the lowest. The
former maximum does not occur where the distribution of the

species varies widely. The shape of the curve is influenced also by the size of the quadrat; and on this account the value of such curves is not very high. The degree of covering of the species is also important.

In order to gain a comprehensive idea of a plant society, it is important not to work with areas which are too small. Now the number of species increases with area according to a logarithmic curve (Fig. 87), so that the area used for observation must not be too great if the dominant species are to be distinguished with certainty.

From the results of a statistical analysis of a plant society, interesting conclusions can be drawn as to the "sociability"
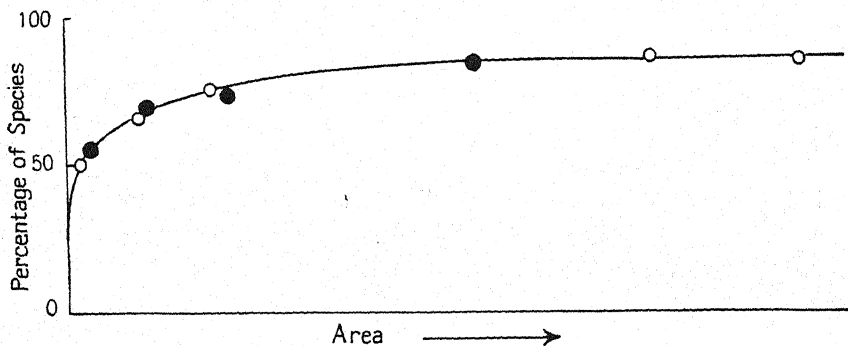
Fig. 87.—Curve showing the relation between area and species number. (After Romell.)

and the fitness for competition of the individuals in the society. (*See also* Rübel, 1922, p. 230.)

In considering the light factor we encountered various examples of differing ecological plasticity. Obligate shade plants and sun plants are not plastic as regards their light requirements; while the facultative shade plants have a wide plasticity in that they can adjust themselves to both light and shade. The same thing is true of the behaviour of plants toward other factors; and it is important for the ecologist to recognize constancy of behaviour of different species toward the various factors of the habitat.

It is naturally tempting to see in the "constancy" of the plant to its society some analogy to the genus concept in floristics—a higher order of association. Closer investigation of plant societies does not, however, lend support to this. For it has to be remembered that the individuals of a plant society are only partly under the influence of the "social factor" in the society. To a great extent they are independent,

and act as individuals toward the environment. From the physiognomic standpoint, "related" plant societies are those which have in common certain dominant species, but to the ecologist, such related societies may be completely different. The occurrence of two species together may be determined in one instance by biotic factors, in another by edaphic, and in a third by climatic factors.

It is evident that it is no easy matter to apply the ecology of the individual plant to the problems of plant sociology. There is no doubt, however, that research into the problems of the individual plant in its habitat is the foundation upon which a causal knowledge of plant sociology must be built.

There are already common names for the great groups of vegetation, which reflect the broad climatic differences of the earth, names which have become adopted into science: rain forest, savannah, steppe, desert, Alpine vegetation, and so on. In their ordinary meanings these concepts are not separable from certain climatic conditions. Similarly, "Mediterranean vegetation," "deciduous forest," and "northern coniferous forest" are quite clear concepts. The common word meadow, on the other hand, may denote a dry meadow, or a boggy meadow, an Alpine meadow or a sea-shore meadow. Here, too, the unprejudiced observer would recognize that the ecological classification, however rough, is the simplest and the most natural. It can be said on the whole that in a competitive plant society the ecological classification is the best. The lover of technicalities, if he pleases, could group all woods as "Lignosa"; there is nothing wrong in the classification, but it is of no particular value.

This clear and obvious broad relationship between the ecological conditions and the type of vegetation, which determines the steppes and prairies, deserts in Sahara and Arizona, Alpine meadows in Switzerland and the Himalayas, probably has its foundation in the mechanism already described for the origin of species. The problems of plant geography merge imperceptibly into purely ecological problems, since the operation of the law of relative effects of the factors is everywhere so evident, that it needs no experiment to observe it.

When one comes to the detailed observation of mesophytic areas, on the other hand, especially when the climatic conditions are fairly uniform, the ecological problems are by no means so obvious. Without extremely careful investigation, it is often impossible to say exactly how the habitat of

specific plants is composed. Two habitats which might, on a superficial observation, be considered identical, will prove, on more careful study, to differ as to the hydrogen ion concentration or the carbon dioxide concentration of the soil atmosphere. A critical analysis of the ecological factors throws an entirely new light upon small differences in the vegetation.

The detailed ecological analysis of an association is, however, an extremely troublesome and tedious undertaking. In competitive societies the dominant ecological factor is easy to determine. But when no factor is clearly in minimum, a very thorough analysis is required, and it is in such instances that the investigator has to be perfectly clear as to the significance of the law of relative effects.

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